Proceedings of the Second International Conference on Copepoda

Ottawa, Canada
13-17 August 1984

G. Schriever, H.K. Schminke and C.-t. Shih, Editors

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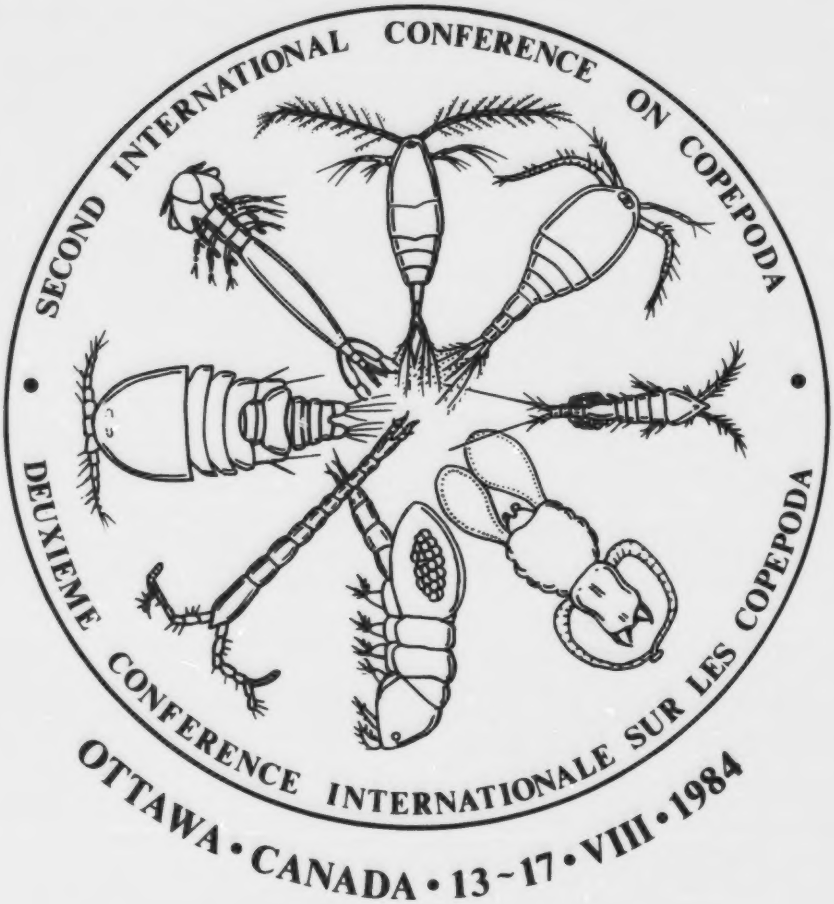
SECOND INTERNATIONAL CONFERENCE ON COPEPODA
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INTRODUCTION

The Second International Conference on Copepoda was held in Ottawa, Canada during the period 13 to 17 August 1984 under the co-sponsorship of the National Museum of Canada and Dalhousie University. The Organizing Committee of the Conference consisted of C.J. Corkett of Dalhousie University (Halifax, Canada), Z. Kabata of the Pacific Biological Station (Nanaimo, Canada), H.K. Schminke of Universität Oldenburg (Oldenburg, F.R. Germany), G. Schriever of Universität Kiel (Kiel, F.R. Germany), C.-t. Shih (chairman) of the National Museum of Natural Sciences (Ottawa, Canada), and J.C. von Vaupel Klein of Universiteit te Leiden (Leiden, The Netherlands). I.R. Sutherland of the National Museum of Natural Sciences chaired the Local Committee.

The programme of the Conference was composed of four symposia, a panel discussion, seven sessions of contributed papers, and a poster session. The responsible author of each presentation was asked to submit a final manuscript to the session chairman at the conclusion of the respective session. The panel discussion was summerized by the moderator based on the tape recorded during the discussion. All session papers received were reviewed by the session chairman and, if necessary, another referee. The accepted manuscripts were then edited by the editors.

The edited manuscripts were typed with the word processor (HERMES TOP-TRONIC VIDEO) by Mrs. K. Knickmeier, Mrs. A. Salewski, Mrs. G. Sütel, and Mr. R. Tiedemann of Kiel under the supervision of G. Schriever and H.K. Schminke. C.-t. Shih, assisted by Mrs. E. Fenton, was responsible for the final production of the proceedings.

The proceedings are divided into four parts: Symposia, Panel Discussion, Contributed Papers, and Posters. The symposium papers are arranged in the same order in which they were presented at the Conference. The contributed papers and posters are, however, arranged according to the alphabethical order of the authors. Some authors did not submit their manuscripts and ohters have already submitted theirs to other journals. For these papers, only the abstracts are included in this volume.

Co-editors: Gerd Schriever
H.Kurt Schminke
Chang-tai Shih

INTRODUCTION

La deuxième Conférence internationale sur les Copépodes s'est tenue à Ottawa (Canada) du 13 au 17 août 1984, sous le coparraigne des Musées nationaux du Canada et de l'Université Dalhousie. Le Comité organisateur de la conférence était composé de C.J. Corkett de l'Université Dalhousie (Halifax, Canada), Z. Kabata de la Station biologique du Pacifique (Nanaimo, Canada), H.K. Schminke de l'Université d'Oldenburg (Oldenburg, République fédérale d'Allemagne), G. Schriever de l'Université de Kiel (Kiel, République fédérale d'Allemagne), C.-t. Shih (président) du Musée national des sciences naturelles (Ottawa, Canada), et J.C. von Vaupel Klein de l'Université de Leyde (Leyde, Pays-Bas). Le Comité local était présidé par I. Sutherland du Musée national des sciences naturelles.

Le programme de la conférence consistait en quatre colloques, une réunion-débat, sept séances de lecture de communications, et une exposition de documents de démonstration. Les auteurs des communications furent invités à présenter au président de la séance un manuscrit définitif au terme de leur exposé. Un résumé de la réunion-débat fut rédigé par l'animateur à partir d'un enregistrement du débat sur bande magnétique. Tous les documents déposés aux séances furent examinés par le président de séance et, au besoin, par un autre arbitre. Les manuscrits acceptés furent ensuite mis au point par l'équipe de rédaction.

Les manuscrit apprêtés furent transcrits à l'aide d'une machine de traitement de texte par M^{me} K. Knickmeir, M^{me} A. Salewski, M^{me} G. Sütel et M. R. Tiedemann de Kiel, sous la supervision de G. Schriever et de H.K. Schminke. C.-t. Shih s'est chargé de la mise au point définitive des comptes rendus, avec l'assistance de M^{me} E. Fenton.

Les comptes rendus sont divisés en quatre parties: colloques, réunion-débat, communications et documents de démonstration. Les documents des colloques sont disposés dans l'ordre de leur présentation à la conférence. En revanche, les communications et les documents de démonstration apparaissent dans l'ordre alphabétique des noms de leurs auteurs. Certains auteurs n'ont pas présenté leurs manuscrits et d'autres ont déjà remis les leurs à d'autres journaux. On ne trouvera dans le présent volume que des résumés de ces études.

Coéditeurs: Gerd Schriever
H. Kurt Schminke
Chang-tai Shih

ACKNOWLEDGEMENTS

We are very grateful to the following institutions and individuals for their various assistance and support given to the Conference:

The National Museum of Natural Sciences provided projectors and other equipment for the meetings, held a reception for the participants, and published the proceedings. The National Sciences and Engeneering Council of Canada awarded a travel grant through Dr. I.A. McLaren of Dalhousie University to partially subsidize travel expenses of some invited speakers from outside North America. The United Nations Education, Science, and Culture Organisation provided two travel grants for participants from the countries where adequate marine science facilities are unavailable. The Zoologisches Institut und Museum der Universität Kiel provided us with the word processor Hermes Video. The staff of the Invertebrate Zoology Division of the National Museum of Natural Sciences, especially Wendy Antoine, Rama Chengalath, Rolande Gaulin, Judith Price, Fahmida Rafi, and Ian Sutherland, helped preparing the conference programme and manning the information desk during the Conference.

We thank several fellow copepodologists who chaired various sessions of the Conference: J.C. von Vaupel Klein (Symposium on Morphology and Anatomy), C.J. Corkett (Symposium on Growth, Life History and Culture), J.-s. Ho (Symposium on Biogeography), B.M. Marcotte (Symposium on Behavioural Ecology), Z. Kabata (Panel Discussion of Copepoda Phylogeny), and the chairmen of seven Contributed Papers session: I. Sutherland, T.K.S. Björnberg, I.A. McLaren, G. Schriever, H.K. Schminke, M. Gophen, and R. Cressey.

The Organizing Committee

REMERCIEMENTS

Nous sommes très reconnaissants aux personnes et aux établissements suivants des diverses formes d'aide et d'appui qu'ils ont apportées à la conférence:

Le Musée national des sciences naturelles a fourni les projecteurs et les autres appareils utilisés durant la conférence, a tenu une réception pour les participants et a publié les comptes rendus des travaux. Le Conseil de recherches en sciences naturelles et en génie du Canada a offert par l'entremise de M. I.A. McLaren de l'Université Dalhousie une subvention destinée à couvrir une partie des frais de déplacement de certain conférenciers invités de l'extérieur de l'Amérique du Nord. L'Organisation des Nations unies pour l'éducation, la science et la culture a fourni deux subventions de voyage destinées aux participants provenant de pays dépourvus d'installations adéquates en sciences maritimes. Les membres du personnel de la Division de la zoologie des invertébrés du Musée national des sciences naturelles, en particulier Wendy Antoine, Rama Chengalath, Rolande Gaulin, Judith Price, Fahmida Rafi et Ian Sutherland, ont aidé à préparer le programme de la conférence et à assurer le service du bureau de renseignements au cours de la conférence.

Nous tenons à remercier nos divers confrères copépodologues qui ont présidé diverses séances de la conférence: J.C. von Vaupel Klein (colloque sur la morphologie et l'anatomie), C.J. Corkett (colloque sur la croissance, le cycle vital et la culture), J.-s. Ho (colloque sur la biogéographie), B.M. Marcotte (colloque sur l'écologie du comportement), Z. Kabata (réunion-débat sur la phylogénèse des Copépodes) ainsi que les présidents des sept séances de lecture des communications: I. Sutherland, T.K.S. Björnberg, I.A. McLaren, G. Schriever, H.K. Schminke, M. Gophen et R. Cressey.

Le Comité organisateur

Symposia

1. Morphology and Anatomy (Chairman: *J.C. von Vaupel Klein*)

ASPECTS OF GENERAL BODY SHAPE AND DEVELOPMENT IN COPEPODA

PATRICIA L. DUDLEY

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Abstract: Examples of pelagic, benthic and symbiontic copepods reaffirm the adaptive nature of body shapes for particular ecological niches. A survey of current usage, however, indicates a need for agreement on the terminology relating to body form and tagmosis. The development of the definitive body shape and tagmosis is traced through ontogeny. Effects of normal and profound allometric modifications, particularly in symbiontic copepods, are evaluated. Fine structural studies on the growth of young adult females of notodelphyid copepods in terminal anecdysis point up the importance of post-moult growth in morphogenesis. The relevance of this process in other copepods is considered. The ontogenetic origin of sexual dimorphism in Copepoda is compared with that in other Crustacea. Dimorphism of males in some notodelphyid species shows how a reversal of a morphogenetic trend can occur. The topography of the body is further explored by using evidence from SEM and TEM on articulations between tagmata, sclerites in metameres, and other anatomical features.

The more than 8000 species of Copepoda (Marcotte, 1983) show an amazing morphological diversity. They range in size from the giant parasite of finback whales, Pennella balaenopterae, which can reach a length of 2 feet (Kabata, 1979) to the minute associate of marine ostracods, Sphaeronellopsis monothrix, whose females are 0.23 mm and males are only 0.11 mm (Kaestner, 1970). The copepods have radiated into many habitats, semi-terrestrial and pelagic, near-benthic, inbenthic and ecto- and endosymbiontic in freshwater, estuarine and marine habitats. Along with this ecological diversity, the copepods have evolved a multitude of body shapes, only a few of which have been studied with respect to their functional significance. In considering this functional significance of body shape, one cannot, of course, divorce the body from its appendages.

Figure 1 is a panorama of some of the body shapes which exist in the Copepoda. The generalized body forms of calanoids (Figs. 1a, b), cyclopoids (Figs. 1c, d) and harpacticoids (Fig. 1e) are familiar to all copepodologists. In the calanoids, there is an obvious difference in width between the fore-body or prosome and the hind-body or urosome and the major body articulation lies behind the segment of the fifth legs. Virtually all of the calanoids are adapted for a pelagic life with their streamlined, rigid, bullet-shaped prosome and a flexible urosome which can be used as a rudder or can "beat" at the frequency of the mouthparts when the animal is maintaining a vertical position in the water column during a feeding bout (Strickler, 1982). The very long first antennae are important in the maintenance of buoyancy (Kabata, 1979). The body shapes of calanoids are much more uniform than those of the cyclopoids or harpacticoids, although fusions of different segments and modifications in rostra, genital segments, and caudal rami provide some variety. Near-benthic species, like species of Pseudocyclops, are smaller in size and have a plumper body and shorter first antennae than the pelagic species (Bowman and Gonzalez, 1961).

Free-living cyclopoids are often near-benthic, although there are some planktonic species too. Their urosome is proportionately longer because the major articulation is set between the segment of the fourth swimming leg and the segment of the reduced fifth legs. Their antennae are much shorter than in the Calanoida. The active swimmers in this group have flexible urosomes and somewhat rigid prosomes, although some slight telescoping of segments is possible. Benthic, crawling cyclopoids have retained more flexibility in their bodies (Kabata, 1979). Many of the cyclopoids and their near relatives among the Poecilostomatoida and the Siphonostomatoida (Kabata, 1979) have become symbionts of other animals. In these copepod associates, the bodies can be relatively unmodified from those of free-living, near-benthic forms or can be significantly modified; some become enormous saccate or lobate forms whose adults are scarcely recognizable as copepods.

Harpacticoids are mainly near-benthic (epibenthic, epiphytic, epizoic) or inbenthic (Marcotte, 1983) although a few are planktonic. Their first antennae are short and their major body articulation is behind the segment of the fourth legs as in cyclopoids. However, most harpacticoids retain considerably more flexibility (Kaestner, 1970). With some exceptions, as for example in species of Tisbe, harpacticoids show a more gradual taper in their bodies and the prosome and urosome are not sharply set off from each other. Some, such as the very flexible vermiform species of Paraleptastacus (Fig. 1f), show virtually no taper and their body outline is almost linear. Discussants of copepod evolution (Kabata, 1979; Marcotte, 1982) believe that the ancestral copepod was benthic or near-benthic and had a trunk in which a prosome was not clearly differentiated from the urosome. Modern benthic harpacticoids are thought to resemble this ancestral copepod more closely than pelagic cyclopoids or calanoids in which a rigid prosome is set off clearly from the urosome.

The other drawings in Figure 1 show body shapes of some other harpacticoids and cyclopoids (and the poecilostome and siphonostome relatives of the latter). Citations to original sources for the drawings are given in the legend of Figure 1. These figures illustrate that it would be difficult to guess exactly where many of these copepods might live on the basis of body shape alone. Appendicular and other adaptations must also be known.

Eudactylopus andrewi (Fig. 1g) is a subcylindrical harpacticoid found in algal washings; Balaenophilus unisetus (Fig. 1h), also has a subcylindrical body shape but its legs and maxillipeds are adapted for holding to baleen strands of blue whales. The body shapes of planktonic harpacticoids may vary from fusiform as in the harpacticoid Macrosetella gracilis (Fig. 1i) to the dorso-ventrally flattened, spatuliform Clytemnestra scutellata (Fig. 1j) and those of planktonic peocilostomatoids vary from dorsoventrally flattened obovoid Sapphirina species (Fig. 1n) to the subclavate Corycaeus limbatus (Figs. 1p, q). While dorsoventral flattening in bodies of some planktonic representatives or the lateral compression in the curious epiphytic or epizoic species of Tegastes (Fig. 1-l) have not, as yet, been explained satisfactorily in a functional sense, dorsoventral flattening in bodies of epibenthic, epizoic forms, which need to hold closely to the substratum, seems clearly adaptive. Dorsoventral flattening is seen, for example, in species of the ovoid harpacticoid Porcellidium (Fig. 1k), some species of which are associated with hermit crabs (P. tapui) while others are dwellers on algae, in siphonostomatoids like Neobradypontius australis (Fig. 1m) which is epibenthic and in parasitic caligids such as the species of Lepeophtheirus (Fig. 1o) in which an almost circular dorsal plate encompasses all of the segments through that of the third leg and enables species to attach to fish. The method of attachment and movement of caligids has been examined in a model paper by Kabata and Hewitt (1971).

Finally, Figures 1r-v show a few of the many unusual body shapes in parasitic poecilostomatoids and siphonostomatoids. Gastrodelphys dalesi (Fig. 1r) has its body modified by the formation of a brood pouch in a greatly enlarged segment of the fourth leg, much as in most representatives of the cyclopoid family Notodelphyidae. In the rough and tumble world of the tentacular crown of polychaetes in which gastrodelphyids live, and in the wave swept environment of the ascidian branchial basket in which one finds notodelphyids, the brood pouch would prevent the loss and ingestion by the hosts of the copepod

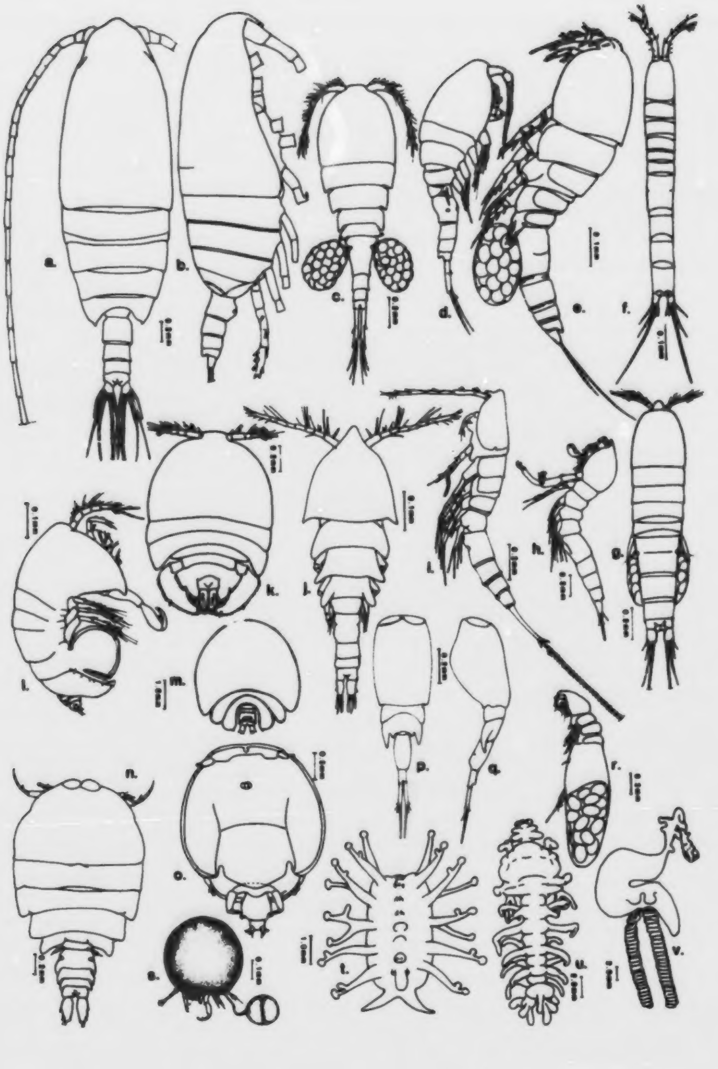


Figure 1. *Examples of body shapes in Copepoda.* **a**, *Undinula vulgaris female, dorsal;* **b**, *Undinula vulgaris female, lateral;* **c**, *generalized freshwater cyclopoid, dorsal,* **d**, *generalized freshwater cyclopoid, lateral;* **e**, *Canthocamptus sp. female, lateral,* *f*, *Paraleptastacus katamentsis female, dorsal (after Wilson, 1932);* **g**, *Eudactylopus andrewi female, dorsal (after Itô, 1974);* **h**, *Balaenophilus unisetus female, lateral (after Vervoort and Tranter, 1961);* **i**, *Macrosetella gracilis female, lateral;* **j**, *Clytemnestra scutellata female, dorsal (after Coull, 1977, and Wilson, 1932);* **k**, *Porcellidium tapui female, dorsal (after Hicks and Webber, 1983);* **l**, *Tegastes acroporanus female, lateral (after Humes, 1981);* **m**, *Neobradypontius australis female, dorsal (after Eiselt, 1962);* **n**, *Sapphirina nigromaculata female, dorsal.* **o**, *Lepeophtheirus scutiger male, dorsal (after Hewitt, 1963);* **p**, *Corycaeus (Agetus) limbatus male, dorsal;* **q**, *Corycaeus (Agetus) limbatus male, lateral;* **r**, *Gastrodelphys dalesi female, lateral (after Dudley, 1966);* **s**, *Choniosphaera cancrorum female lateral (after Johnson, 1957);* **t**, *Linaresia mammillifera female, ventral (after Bouligand, 1966);* **u**, *Philichthys xiphiae female, dorsal (after Ho, 1978);* **v**, *Haemobaphes cyclopterina female (after Delamare Deboutteville and Nunes Ruivo, 1955).*

embryos before they are ready to hatch and swim. The elongate body of the gastrodelphyid female may help to provide camouflage among the tentacles of the worm. The spherical shape of Choniosphaera cancrorum (Fig. 1s), along with its color, may also serve as camouflage for the copepod among the eggs of a crab which it parasitizes. Similarly, the capitate arms of the greatly modified Linaresia mammilifera (Fig. 1t) look something like the tentacles of the gorgonian polyp which this parasite occupies. Many of the parasites of fish such as Philichthys xiphiae (Fig. 1u) and Haemobaphes cyclopterina (Fig. 1v) are saccate or lobate, the results of allometric growth after the last molt which increases the body volume for egg production and storage or prevents the dislodgement of the parasite from its host (Kabata, 1979).

Despite the somewhat enigmatic proliferation of body shapes of copepods, there is a basic unity in most cyclopoids, calanoids and harpacticoids in the numbers of body segments, if not in adults then in developmental stages. Exactly how these body segments are arranged in tagmata, however, is not at all agreed upon by all investigators. This discussion now turns to an examination of various ideas on tagmosis, as well as how tagmosis arises in development and how tagmata are modified. Sexual dimorphism, stepless allometric growth, and host-parasite interactions also affect body shape and will be briefly discussed.

TERMINOLOGY FOR BODY REGIONS

It is very difficult to find a consensus as to the correct terminology for segmentation and tagmosis in the copepods. I have found as Illg (1958) did, that the number of schools of thought on the subject almost equals the number of authors. There are, however, a few systems of terminology that are more common than others and I have diagrammed these in Figure 2. Acceptable to many investigators is the idea (Giesbrecht, 1892) that there is a major dichotomy in the Copepoda between Gymnoplea (= Calanoida), in which there are no appendages on the segments posterior to the major articulation, and "podoplean" copepods (= all copepods except the Calanoida), in which there are reduced appendages - fifth and sixth legs - on body segments posterior to the major body articulation. In parasites this may be apparent only in copepodid stages. Although the idea of a dichotomy is accepted by many and is reinforced by a study of development in the two groups, Gymnoplea and Podoplea are only rarely used as categories in classification schemes today.

Much of the difficulty in reaching an agreement on the terminology for body regions derives from the following: (1) the utilization by some authors of a nomenclature that relates to a theoretical homology of metameres and tagmata of copepods which those of other crustaceans, in particular with those of malacostracans. The limits of the tagmata so defined do not coincide with the "real" and observable boundaries of functional groups of metameres in copepod bodies; (2) the utilization by other authors of a practical terminology or terminology of convenience which names the major body regions of copepods without relating them to an homology with other crustaceans and only concerns itself with major observable functional divisions. However, the major functional divisions do not necessarily contain the same numbers of metameres in all copepods; and (3) the use of a mixture of terms from both the "theoretical" (1) and the "practical" (2) terminology.

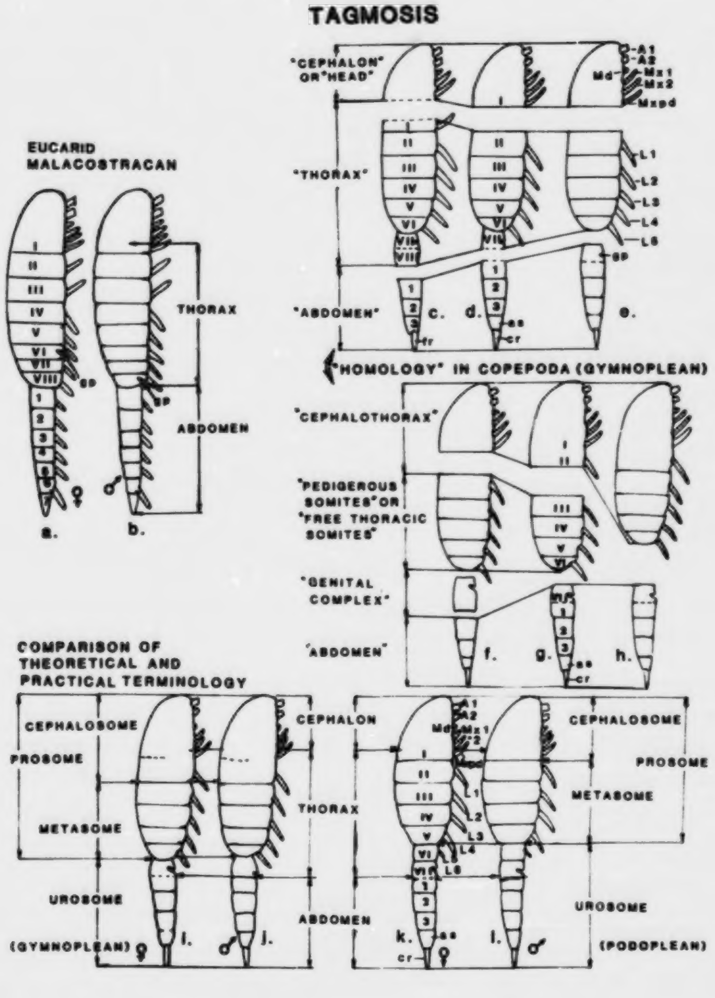

TAGMOSIS
"CEPHALON" OR "HEAD"
A1
A2
Md
Mx1
Mx2
Mxpd
"THORAX"
L1
L2
L3
L4
L5
GP
"ABDOMEN"
c.
d.
e.
as
cr
EUCARID MALACOSTRACAN
THORAX
ABDOMEN
a.
b.
"HOMOLOGY" IN COPEPODA (GYMNOPLEAN)
"CEPHALOTHORAX"
"PEDIGEROUS SOMITES" OR "FREE THORACIC SOMITES"
"GENITAL COMPLEX"
"ABDOMEN"
f.
g.
h.
COMPARISON OF THEORETICAL AND PRACTICAL TERMINOLOGY
CEPHALOSOME
PROSOME
METASOME
UROSOME
(GYMNOPLEAN)
i.
j.
CEPHALON
THORAX
ABDOMEN
k.
l.
(PODOPLEAN)

Figure 2. *Nomenclature for tagmosis in Copepoda.* **a**, *Diagram of female eucarid malacostracan, showing the cephalon, eight thoracic segments (I-VIII), six abdominal segments and telson (1-7); The genital pore (g.p.) is on the sixth thoracic segment.* **b**, *Diagram of male eucarid malacostracan for comparison with copepods. Genital pores are on the eighth thoracic segment.* **c-h**, *Diagrams illustrating various nomenclatural schemes for copepod tagmosis based on supposed homologies with malacostracan crustaceans as found in the literature. Explanation in text.* **i-l**, *Diagrams comparing the use of terminology for tagmata based on homology and "practical" terminology which divides the body according to function rather than on the basis of homology with malacostracan tagmata. Explanation in text.*

Theoretical terminology relating to homology

Diagrams of female and male eucarid malacostracans (Figs. 2a, b) are given for comparative purposes. There seems to be little difficulty in homologizing the anteriormost appendages of Copepoda with those of the Malacostraca, but it is in the more posterior segments that attempts at homology go awry. The "exploded" diagrams in Figures 2c-h show some of the ways in which tagmata of gymnoplean copepods have been interpreted and Table 1 lists the ways in which body segments have been apportioned to various tagmata by a sample of authors. An explanation of the terminology is given below. An excellent summary of problems of nomenclature in copepod tagmosis, which includes much more material than can be included here, can be found in von Vaupel Klein (1982).

Cephalon

No crustacean has more than five pairs of appendages (antenna 1, 2; mandible; maxilla 1, 2) on its head or cephalon (Figs. 2c, i-l). The next pair of appendages in anteroposterior sequence, the maxillipeds, must belong to the thorax (Gurney, 1931, p.33). However, Gurney (1931, p.36), Rose (1933), Corkett and McLaren (1978), and von Vaupel Klein (1982) refer to the cephalon or head as including the segment of the maxillipeds (Figs. 2d, e). Some investigators have even stated that "the head is regarded as a single segment" (C.B. Wilson, 1932). Such designations are confusing, even if meant only in a descriptive sense.

Thorax

Gurney (1931) in his figures 2 and 3 and discussion, p.34, postulated that copepods might have 8 thoracic segments as do the Malacostraca (Fig. 2c). In this case, the abdomen would be very short and the genital complex in females would be formed of two thoracic segments. However, the genital pores of both male and female copepods would be on the seventh thoracic segment which does not coincide with the placement of the thoracic genital pores in Malacostraca. Illg (1958) and Dudley (1966) are representatives of the school (Figs. 2i-l) which believes that maxillipeds are appendages of the first thoracic segment and that the thorax ends at the genital segment (Th VII) - the most posterior segment to have limbs (sixth legs) in podoplean copepods. According to this school, the genital complex of the female would be a composite of the last thoracic segment and the first abdominal segment. Using a terminology of convenience by including the maxillipedal segment in the cephalon, Corkett and McLaren (1978) define a thorax of only six segments, ending with the genital segment (Fig. 2d). The genital complex in females is formed of the last thoracic and the first abdominal segment. Newman (1983), in a discussion of the origin of the Maxillopoda, also considers the thorax to have six segments but the anterior and posterior limits differ from those of Corkett and McLaren (1978). Thus, Newman includes the maxillipedal segment in the thorax but relegates the seventh thoracic and genital segment to the abdomen. Finally, some investigators (Gurney, 1931, p.36; Rose, 1933) have made as Gurney stated "a compromise between custom, convenience and homology" and consider the maxillipeds to be appendages of the head, the thorax to consist of only the five leg-bearing segments (in calanoids) and the abdomen to be all of the body posterior to the major body articulation, including the genital complex (Fig. 2e).

In some copepods, fusion of body segments during development can reduce the number of observable thoracic segments (as in the fusion of the fourth and fifth leg-bearing segments in many calanoids, as for example in Aetideus) (Owre and Foyo, 1967) or articulations between segments and some appendages can be lost, as in many parasites, making the attribution of segments to particular tagmata even more difficult than in free-living representatives.

In all of the ideas about the segmetal composition of the thorax (except that of the 8-segmented thorax), the copepod is believed to have fewer segments in this tagma than in the Malacostraca. Most modern theories of the evolution of the Copepoda derive them by progenetic and neotenic paedomorphosis from larval malacostracans or urmalacostracans (Gurney, 1942; Marcotte, 1982; Newman, 1983). The shortened thorax could have resulted from the arrested development of the limbs of the last thoracic segment(s) and the abdominalization of the limbless segment(s). The shortened abdomen, with fewer segments than in the malacostracan adult, could have resulted from precocious maturation before a full complement of abdominal segments was formed by the zone of growth.

Abdomen

Since the abdomen of a copepod is a limbless tagma posterior to the thorax, the number of segments included in it depends on the posterior limit placed on the thorax. It can have 3-5 segments, depending on how many segments the thorax is said to have (Table 1). Some authors (Owre and Foyo, 1967; Kabata, 1979; Jones in Monoculus Nr. 6, 1983) consider the genital complex of females and the genital segment of males as separate from both the abdomen and the thorax (Fig. 2f). The caudal rami at the posterior end of the abdomen seem to be derived from the telson and cannot, therefore, be considered to be uropods as proposed by Bowman (1971).

Table 1: *Distribution of body segments in tagmata of Copepoda compared with eucarid Malacostraca (Numbers in cephalon, thorax and abdomen columns refer to number of body segments proposed for tagmata; A and Arabic numerals = segments of abdomen; Ap = appendages; As = anal segment or telson; G.C. = genital complex of female copepod; G.S. = genital segment; G = gymnoplean copepod; P = podoplean copepod; Th and Roman numerals = thoracic segments.)*

Reference and Animal	Figure	Cephalon	Thorax	Abdomen	G.C. Fem.	G.S. Male
Malacostraca:						
Gurney, 1931	2a, b	5	8	7 (6 + T)	ThVI (G.P.)	ThVIII
Copepoda:						
Gurney, 1931 (pt)	2c (G)	5	8	3 (2 + AS)	ThVII + ThVIII	ThVII
Dudley, 1966	2i-l (G, P)	5	7	4 (3 + AS)	ThVII + AbI	ThVII
Newman, 1983	none	5	6	5 (4 + AS)	Ab 1 (G.P.)	Ab 1
Corkett & McLaren, 1978	2d (G)	6	6	4 (3 + AS)	ThVI + Ab 1	ThVI
Gurney, 1931 (pt);	2e (G)	6	5	5 (4 + AS)	-	Ab 1 = Th?
Wilson, 1932	none	1 (5 Ap)	7	4 (3 + AS)	ThVII + Ab 1	ThVII

Cephalothorax

In its narrowest sense, this term has been used (Illg, 1958) to refer to an anterior body complex including the segments of the cephalon and the maxillipedal segment as the only thoracic element (Fig. 2f). It has also been defined (Fig. 2g) as an anterior section which includes the cephalon, the maxillipedal segment and one or more leg-bearing segments (Wilson, 1932; Gooding, 1957; Kabata, 1979). In its broadest sense, the cephalothorax is considered (Sewell, 1947) to be equivalent to "Prosome", that is, to all of the body anterior to the major body articulation (Fig. 2h). Those who consider the cephalothorax to be more restricted in its composition refer to the leg-bearing segments

Practical terminology

Using this terminology for tagmata, the copepod body is divided into a **cephalosome**, **metasome** and **urosome**. This nomenclature is usually easier to use than the theoretical terminology above, particularly if some latitude is given as to the posterior limit of the cephalosome. In using these terms, Corkett and McLaren (1978), von Vaupel Klein in Monoculus Nr. 5 (1982), and Corkett and Shih in Monoculus Nr. 8 (1984) consider the **cephalosome** to be a fused complex of the head, maxillipedal segment, and, sometimes, additional leg-bearing segments (Figs. 2i, j). However, in its original definition (Sars, 1901), the cephalosome was limited to the fused complex of the cephalon and the segment of the maxillipeds only (Figs. 2k, l) and some modern investigators still restrict the definition in this way (Gooding, 1957; Kabata, 1979, Jones in Monoculus Nr. 6, 1983; Matthews and Fosshagen in Monoculus Nr. 8, 1984). The **metasome** includes the pedigerous segments between the cephalosome and the major body articulation (Figs. 2i-l). Its anterior limit depends on the definition given to the cephalosome. If the restricted definition of the cephalosome is used, the metasome would include pedigerous segments that are included in the anterior fused section, as well as free pedigerous segments. With the broader defintition of cephalosome, which includes all segments fused with the head, the metasome would be only the free pedigerous segments between the fused anterior section and the major body articulation. The **urosome** is the part of the body posterior to the major body articulation (Figs. 2i-l). The term **Prosome** (Gooding, 1957) is a useful term for the entire body in front of the major body articulation (Figs. 2i-l). It includes both the cephalosome and the metasome.

Although this "practical" terminology is more flexible than the theoretical terminology described above, particularly if a broad definition is given to the cephalosome, it has the obvious fault that a metasome or a urosome in one copepod may not be exactly equivalent to those in another because of different degrees of cephalization of metasomal segments or because the major body articulation falls at different levels as in the generalized gymnopleans and podopleans or in some modified podopleans such as the caligids (where it lies between the third and fourth leg-bearing segments). However, when precise limits are given in the definitions of the tagmata, we have the same problem we had with the use of the theoretical terminology because defined boundaries fall at positions in the bodies of different copepods that do not always delimit observable functional regions. Too, if this terminology is used, it should be recognized that it is somewhat tainted as far as its history is concerned. The author of this terminology (Sars, 1901) believed that the mesosome (thorax minus the segment of the maxillipeds) was suppressed in copepods and that the metasome and urosome he proposed were really subdivisions of a part of the body comparable to the abdomen of a malacostracan. Also, the word metasome has been used by some investigators to denote the entire body anterior to the main articulation, thus making it synonymous with "prosome" (C.B. Wilson, 1932; M.S. Wilson and Yeatman, 1958; Illg, 1958).

Mixed terminology

Some investigators use a mixture of terms from the theoretical terminology and the practical terminology. Examples of this would be the use by Owre and Foyo (1967) of cephalothorax, thorax, and urosome and the use by von Vaupel Klein (1982) of cephalothorax (*sensu lato*) and urosome.

Development of Tagmosis: It is interesting to look at the development of relatively unmodified calanoids, cyclopoids and harpacticoids to see how the tagmosis of the body originates and changes through ontogeny. Only three pairs of primitive appendages, antennules, antennae, and mandibles, and primordia of six postmandibular appendages give any external evidence that the nauplius is metameric.

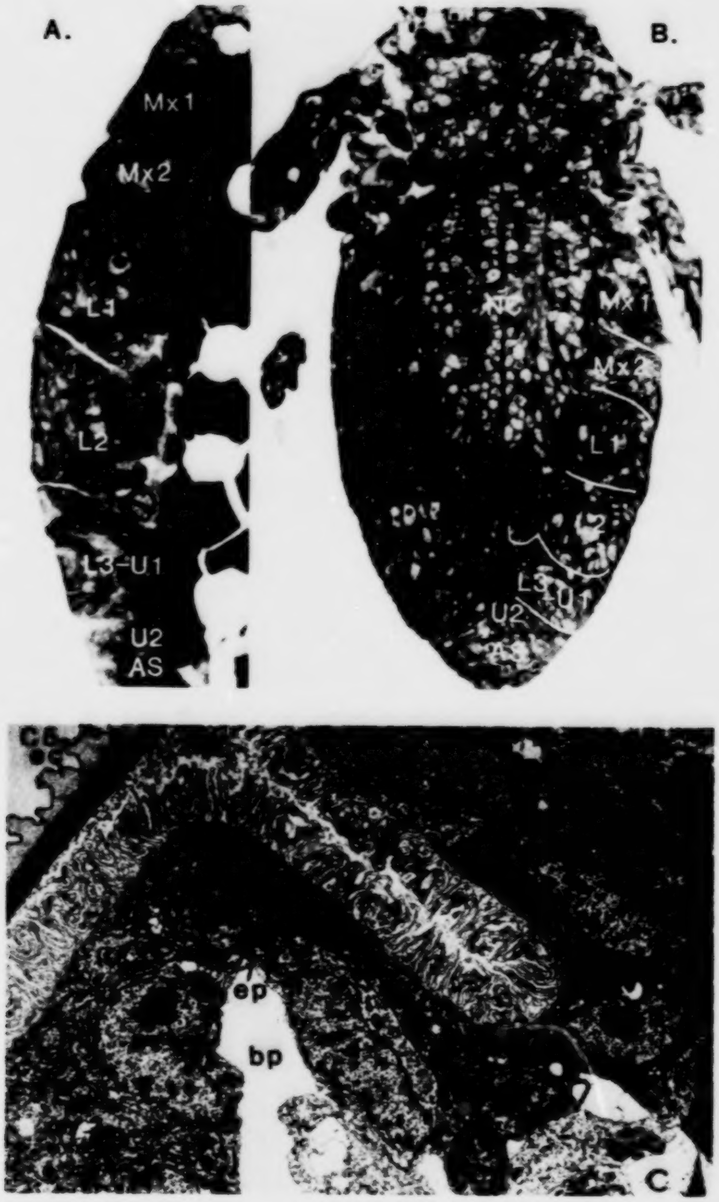
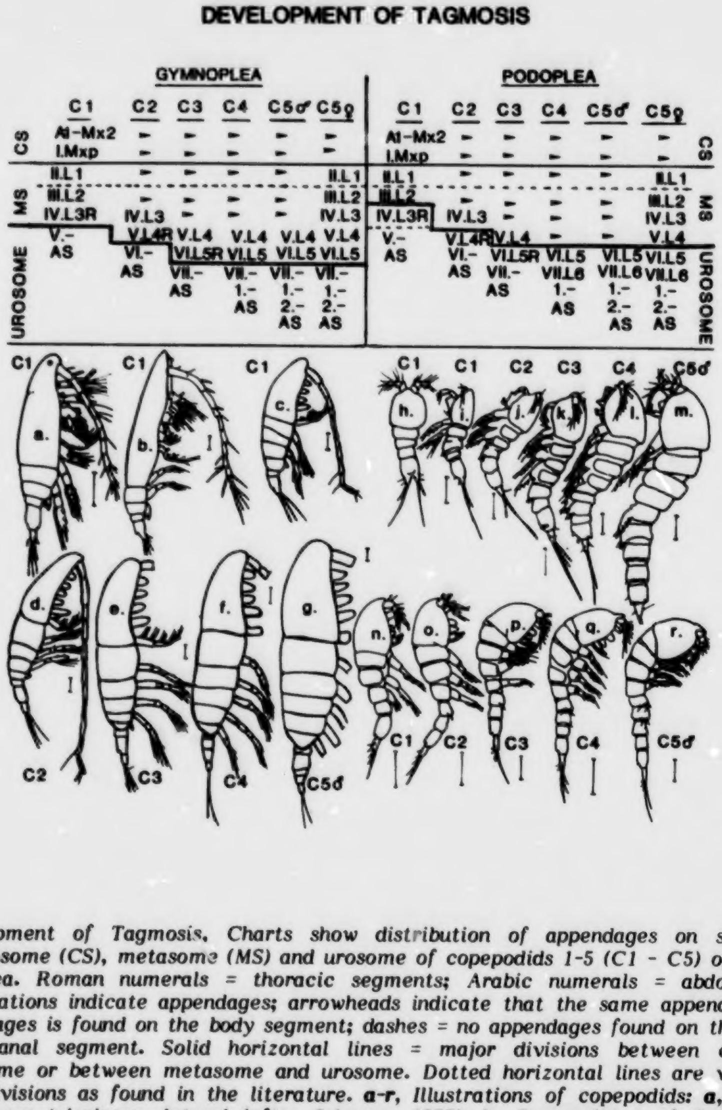


Figure 3. **A.** *Light micrograph, parasagittal section of ventral surface of first nauplius of Doropygus seclusus (3 hours after eclosion); x950.* **B.** *Light micrograph, ventral frontal section of second nauplius of Doropygus seclusus (17 hours after eclosion); x550. Developing appendages and segments are indicated. NC = nerve cord; Mx1 and 2 = first and second maxillae, L1,2,3 = legs; U1, U2 = urosomal segments; AS = anal segment.* **C.** *Portion of a parasagittal section of the developing dorsal brood pouch wall of a late fifth copepodid female of Notodelphys affinis. The cuticle of the last metasomal segment (ec) has loosened from the underlying greatly folded developing cuticle of the adult female (CVIec) and a molting space (ms) is present. The cavity of the brood pouch (bp) is just opening and is not yet lined with cuticle. x5000.*

Except for the grouped primitive appendages near the anterior end, there is no evidence of tagmosis and only the protruding parts of the developing postmandibular appendages leave an indication on the exuvium (Dudley, 1966). In notodelphyid nauplii which I have studied, however, there is a cryptic development of metameres in the body, so that from the time of hatching, blocks of tissue comprising the body segments of the first copepodid are already present and continue to develop through all of the naupliar stages. These segmental blocks do not show on the cuticular exuvia, however, because they are mainly subsurface units and can only be fully studied in histological sections. Figures 3 A, B show such metameric blocks in sections of first and second nauplii of Doropygus seclusus. Because of the cryptic development of segments, the molt to the first copepodid is not as metamorphic as many investigators believe. I do not know definitely that such a process of development of body segments occurs in other groups of copepods but I suspect that it does and students of post-eclosional development in copepods should not restrict their studies to the external cuticle alone.

The charts and illustrations of the development of tagmosis in copepodid stages in Figure 4 are based on information from Johnson (1935, 1937) on the development of species of Labidocera (Fig. 4a) and Eucalanus elongatus (Fig. 4b), from Campbell (1934) on the development of Calanus tonsus (Figs. 4c-g) from Itô and Takashio (1981) on the development of Canthocamptus mirabilis (Figs. 4h-m) and from Dudley (1966) on the development of Notodelphys affinis (Figs. 4n-r). The charts trace my interpretation of the development of tagmosis in these species. However, it is as difficult to interpret these authors' ideas about tagmosis and the positions of the major body articulation at different copepodid stages as it sometimes is to understand the terminology used for adult copepods. Only with histological studies and combined functional analyses could we be sure about how the body articulation changes during ontogeny. The following points can be made about the development of body segmentation and tagmosis: (1) all of the copepods pictured have the same number of metameres at each particular copepodid stage. One new posterior metamere is added in front of the anal segment at each molt; (2) The cephalosome (defined as the zone bearing appendages from A1 to Mxp) had its complete complement of appendages at the first copepodid stage. If the broad definition of cephalosome is used and a fused first legbearing segment is considered part of this tagma (dotted line following the segment of leg 1 on the chart), only Calanus tonsus among the calanoids added a segment late in development while the other two species of calanoids already had the first leg segment fused at the first copepodid stage; (3) The metasome reached its full complement of metameres at the third copepodid stage in both podopleans and gymnopleans. Because podopleans have one less segment in their prosomes than the gymnopleans, it has long been thought (Calman, 1909) that the prosome-urosome articulation became fixed in the podoplean second copepodid stage but didn't reach its definitive position in gymnopleans until the third copepodid stage. This does not seem to be true; (4) The urosome, along with the fusions characteristic of adults, is not completed until the molt of the fifth copepodids to adults; (5) Between the first and the third copepodid stages, only thoracic segments are formed by the zone of growth. After the third copepodid stage, one new abdominal segment is added at the zone of growth at each copepodid stage; (6) The bodies of the copepodids, from the earliest copepodid stage, are easily recognizable as podoplean or gymnoplean, and, on the basis of general body shape, as calanoids, harpacticoids, or cyclopoids. Some, such as Eucalanus and Canthocamptus, are recognizable to genus. Appendicular characters are not considered here, but would undoubtedly permit more precise identifications.



DEVELOPMENT OF TAGMOSIS
GYMNOPLEA
PODOPLEA
C1
C2
C3
C4
C5♂
C5♀
CS
MS
UROSOME
AI-Mx2
I.Mxp
II.L1
III.L2
IV.L3R
IV.L3
V.-
AS
V.L4R
V.L4
VI.-
VI.L5R
VI.L5
VII.-
VII.L6
1.-
2.-
a.
b.
c.
d.
e.
f.
g.
h.
i.
j.
k.
l.
m.
n.
o.
p.
q.
r.

Figure 4. *Development of Tagmosis. Charts show distribution of appendages on segments of the cephalosome (CS), metasome (MS) and urosome of copepodids 1-5 (C1 - C5) of Gymnoplea and Podoplea. Roman numerals = thoracic segments; Arabic numerals = abdominal segments; abbreviations indicate appendages; arrowheads indicate that the same appendage or series of appendages is found on the body segment; dashes = no appendages found on the body segment; AS = anal segment. Solid horizontal lines = major divisions between cephalosome and metasome or between metasome and urosome. Dotted horizontal lines are variants of major body divisions as found in the literature.* **a-r**, *Illustrations of copepodids:* **a**, *Copepodid 1 of Labidocera trispinosa, lateral (after Johnson, 1935);* **b**, *Copepodid 1 of Eucalanus elongatus var. bungii, lateral (after Johnson, 1937);* **c-g**, *Copepodids 2 - 5 of Calanus tonsus, lateral (after Campbell, 1934);* **h**, *Copepodid 1 of Canthocamptus mirabilis, dorsal (after Itô and Takashio, 1981);* **i-m**, *Copepodids 1 - 5 of Canthocamptus mirabilis, lateral (after Itô and Takashio, 1981);* **n-r**, *Copepodids 1 - 5 of Notodelphys affinis, lateral (after Dudley, 1966).*

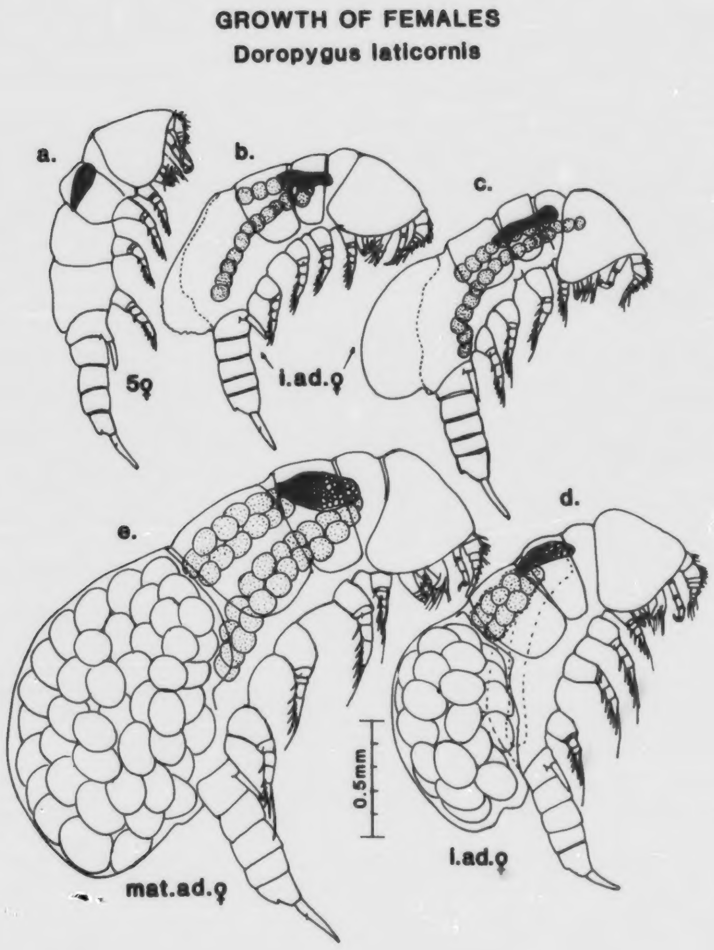

GROWTH OF FEMALES
Doropygus laticornis
a.
b.
c.
5♀
l.ad.♀
e.
d.
0.5mm
l.ad.♀
mat.ad.♀

Figure 5. *Growth of females of* *Doropygus laticornis.* ***a****, Fifth copepodid female, lateral view.* ***b-e****, Stages of growth of females after the terminal molt, showing the enlargement of the metasome with brood pouch. The scale refers to* ***a-e****.*

Allometric Post-ecdysial Growth: One of the factors that can affect the body shape of adult copepods is allometric growth after the final molt, a type of growth that Kabata (1981) refers to as continuous and stepless and Gotto (1979) as extra-ecdysial growth. Kabata (1979, 1981) discussed in detail the morphological transformations by allometric growth that occur in many poecilostome and siphonostome parasites of fish after the cessation of the molting process. This type of growth can involve differently phased transformations of attachment organs and reproductive parts of the body. This type of growth apparently does not occur in freeliving copepods, but the formation of asymmetrical genital segments in some calanoids after the last molt (von Vaupel Klein, 1982) might be similar in some regards. Among symbiotic copepods, it appears to be common. Bocquet, Guillet and Stock (1958) and Kabata (1967) showed that processes of the second through fourth thoracic segments of Nicothoe astaci grow without the necessity of a molt and Laubier (1965) has shown extra-ecdysial growth in Nereicola ovatus. Finally, I have shown (Dudley, 1966) that there is a great increase in the lengths of adult females of notodelphyid copepods after their final molt. The increase in size occurs primarily in the metasome and the segments involved in the formation of the brood pouch and the production and storage of eggs. There also is some growth of the cephalosome and urosome, but less than in the metasome. A fifth copepodid female and various adult females of Doropygus laticornis are shown in Figure 5 to illustrate the pattern of growth of the metasome and brood pouch.

As Kabata (1981) and Gotto (1979) point out, this type of growth has interesting implications with respect to what is known about cuticle formation and the normal step-like growth of arthropods in general. Little is known about the mode of cuticle formation under these circumstances. It is not known whether this type of growth is due to the actual mitoses of cells or due to the enlargement of existing cells. In either case, the cuticle has to be pliable or needs constant increments or both. Figure 3 C shows a section of the last metasomal segment (4th leg-bearing segment) of a fifth copepodid female of Notodelphys affinis. It is in this already swollen segment that the brood pouch will begin its formation. Epidermal cells proliferate and the cavity of the brood pouch forms as a split in the middle of the dorsal and lateral epidermal layers. Figure 3 C shows the deeply invaginate pattern of the wall of the adult's brood pouch as it forms under the cuticle of the fifth female stage. The rugose nature of the cuticle of both the fifth female and that of the forming brood pouch wall of the adult should be noted. The nature of this cuticle is quite different from reports of cuticular structure in the literature. At the fifth stage shown, the brood pouch cavity has not fully formed although some spaces are apparent beneath the epidermal layer. In the adult female of Notodelphys affinis, the brood pouch wall (Figs. 6A-C) has a rugose external cuticle and a thinner rugose cuticle lining the pouch. Tonofibrils in epidermal cells form stabilization pillars at intervals across the outer wall of the brood pouch and glands of many kinds occupy the area between the epidermal layers of the brood pouch vault. Microtubules form a possibly supporting layer within the layer of epidermal cells adjacent to the lining of the pouch. No mitotic figures have been seen within the epidermal cells and it is therefore suggested that the enlargement of the brood pouch occurs by stretching and enlargement of existing cells rather than by increments of cells. Numerous vesicles are adjacent to the lining cuticle, perhaps indicating an exocytotic addition of cuticle as needed. Does the rugose nature of both outer and inner cuticles indicate that these layers can stretch during the growth of the brood pouch?

Sexual Dimorphism: The gender of the copepod obviously affects its morphology. Examples of this are secondary sexual differences in the genital segments and the presence in many males of geniculate first antennae (only one geniculate in some calanoids, both geniculate in many cyclopoids or harpacticoids) or

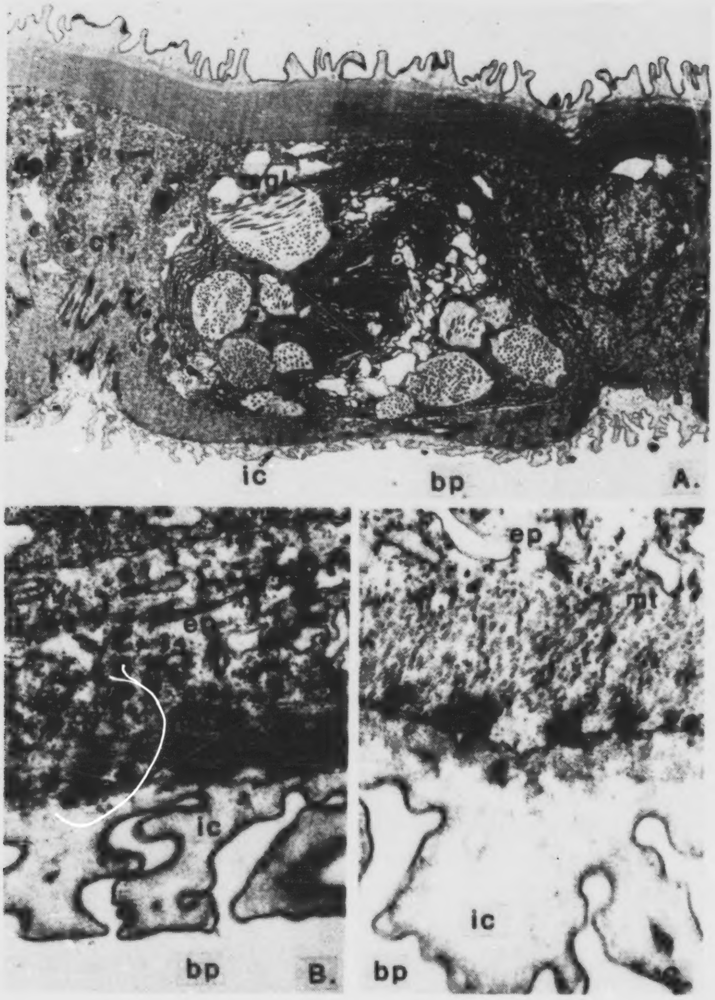


Figure 6. ***A.*** *Parasagittal section through brood pouch wall of a young adult fifth copepodid female of Notodelphys affinis. The brood pouch cavity (bp) does not contain embryos. Both the external cuticle (ec) and the cuticle lining the brood pouch (ic) are rugose. At intervals along the wall, pairs of epidermal cells, containing tonofibrils (cf), stabilize the pouch. Glands, such as mucus glands (mgl) are abundant in the area between the outer and inner walls of the brood pouch. x4900.* ***B.*** *Parasagittal section of inner brood pouch wall of young adult female of Notodelphys affinis showing the microtubular layer (mt) in the epidermal cells (ep) overlying the inner cuticle of the brood pouch wall (ic); bp = cavity of brood pouch. x26000.* ***C.*** *Inner cuticle and epidermis with microtubular layer in a parasagittal section of the brood pouch wall of a young adult female of Notodelphys affinis. Vesicles (V) dot the cell membrane of the epidermal cells. Other labels as in Fig. 9B. x31000.*

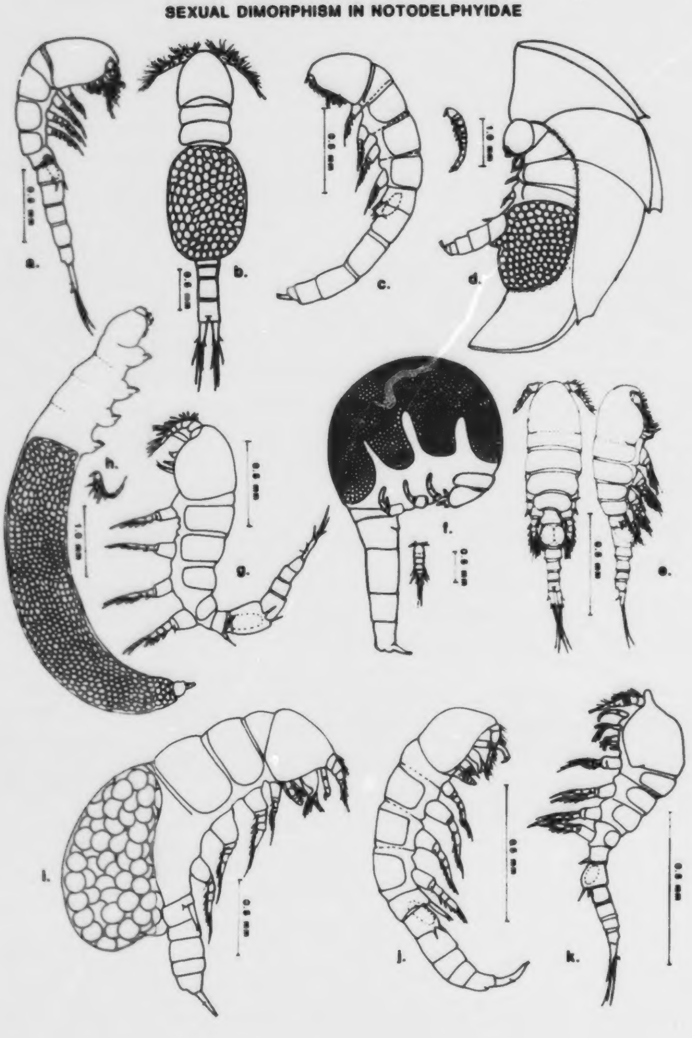


Figure 7. *Sexual dimorphism in Notodelphyidae.* **a**, *Male of Notodelphys affinis, lateral (after Dudley, 1966);* **b**, *Female of Notodelphys affinis (after Illg, 1958);* **c**, *Male of Notopterophorus elatus, lateral;* **d**, *Female of Notopterophorus elatus, lateral; adjacent male is drawn at same scale as female.* **e**, *Lateral and dorsal views of male of Gunetotophorus globularis;* **f**, *Female of Gunetotophorus globularis with adjacent small male drawn at same scale as female;* **g**, *Male of Scolecodes huntsmani, lateral;* **h**, *Female of Scolecodes huntsmani, lateral, with small male drawn at same scale;* **i**, *Female of Doropygus laticornis, lateral;* **j**, *Anamorphic male of Doropygus laticornis, lateral;* **k**, *Metamorphic male ("Agnathaner"-type), lateral.*

the adaptations of male fifth legs for copulation in calanoids (Owre and Foyo, 1967) or the enlargement of the male's maxillipeds in some poecilostomes (Illg, 1960). However, some sexually dimorphic features of body shape are not understandable in terms of sexual function and possibly indicate some major differences in life habits of the male and the female. Thus, why are the body shapes and eyes of the males and females of species of Sapphirina and Copilia so different (Owre and Foyo, 1967)? Why do rostra of males and females of Aetideus armatus and species of Oithona differ so greatly? Why do females of Calocalanus pavo have beautifully plumose caudal rami which are held at virtual right angles to the urosome, while males have parallel and unplumed caudal rami?

An interesting collection of types of sexual dimorphism is seen in the family Notodelphyidae. Examples are given in Figure 7. Within the family, some species have cyclopoid swimming males with mouthparts like those of the females, as in Notodelphys affinis (Figs. 7a, b) while others have cyclopoid swimming males but with attenuate, setose, reduced mouthparts as in Gunenotophorus globularis (Figs. 7e, f) and Scolecodes huntsmani (Figs. 7g, h). Still others, such as Notopterophorus elatus (Figs. 7c, d) have only males with stiffened bodies and shortened setae on legs and caudal rami. These males are incapable of swimming. Still other species have two kinds of males, a swimming cyclopoid male with attenuate setose mouthparts and a crawling male whose mouthparts are not reduced. I reported this male dimorphism in Doropygus seclusus (Dudley, 1966) and have subsequently found it also in Doropygus laticornis (Figs. 7i, j, k). Hipeau Jacquotte (1980a, b) has shown a similar male dimorphism in Pachypygus gibber and her studies of development show that the development of the "atypical" swimming male occurs in younger hosts than the development to the "typical" crawling male. Except for two cases in which swimming males were found inside the hosts, I have only obtained the swimming type males when I have removed fifth copepodid males from hosts and placed them in sea water. Thus, the hosts seem to exert a definite effect on the direction of development. The development of swimming males in the species of Doropygus appears to rapidly reverse a pattern of degenerative changes which have been occurring in the bodies but not the mouthparts of younger copepodid stages. It seems unlikely that the swimming males of species of Doropygus or those of Scolecodes or Gunenotophorus can feed. It apparently is an advantage to have a shortlived swimming male which can move through the water to other ascidians where there may be unmated females or fifth copepodid females ready to molt to the adult, but not to males. This study is continuing.

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ASPECTS OF INTERNAL ANATOMY AND REPRODUCTION IN THE COPEPODA

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Abstract: The functional morphology of the muscular, digestive, circulatory, and nervous systems is reviewed and compared in the Copepoda, with emphasis on the Calanoida. Recent ultrastructural data are provided with respect to the reproductive system in marine calanoids.

Paired dorsal and ventral longitudinal muscles constitute the main muscle bands of both the metasome and urosome. The digestive tract consists of a mouth, esophagus, midgut, hindgut, and an anus. The extensive midgut is morphologically divided into three zones characterized by various cell types. A simple heart enclosed in a large pericardial cavity comprises part of the open circulatory system. Hemolymph flows from an anteriorly directed aorta through various sinuses in the head. These are continuous with the perivisceral cavity, from which the hemolymph is returned to the pericardial cavity. The nervous system consists of a brain, a ventral nerve cord with ganglia in each metasomal segment, and a giant nerve network.

The male reproductive tract is composed of a single testis and a genital duct which is divided into the ductus deferens, seminal vesicle, spermatophore sac, ductus ejaculatorius and gonopore. Spermatogenesis results in disc-shaped, aflagellate spermatozoa that lack acrosomes. In the female, a single ovary extends into two oviducts that terminate at a pair of spermathecae and a single genital opening. Yolk formation in the developing oocytes involves both autosynthetic and heterosynthetic processes.

INTRODUCTION

The study of the internal anatomy of copepods has been neglected relative to other aspects of their biology and life history such as feeding, behavior, development and growth. Morphological descriptions of all the internal systems in any one copepod are rare. The morphology of *Cyclops* was studied by Hartog (1888), and later Fahrenbach (1962) utilized histological methods to elucidate the details of the internal anatomy of the harpacticoid *Diarthrodes cystoecus*. With respect to the Calanoida, the anatomy of *Calanus finmarchicus* was first described by Lowe (1935) whose work was later reviewed by Marshall and Orr (1955). Park (1966) presented extensive details on the anatomy of a pontellid, *Epilabidocera amphitrites*, by examining serial sections. Some ultrastructural aspects of the internal anatomy of *C. finmarchicus* were later contributed by Raymont et al. (1974).

It is beyond the scope of this paper to describe the internal anatomy of all copepod orders. Therefore, the following discussions will review the work of other authors. Emphasis here will be on the Calanoida, but occasional comparisons with other free-living copepods and incidental references to parasitic forms will be included, in addition to relatively new material on gametogenesis in a pontellid calanoid.

METHODS

To illustrate ultrastructural features of the internal anatomy in copepods, the calanoids *Labidocera aestiva*, *Undinula vulgaris*, *Pleuromamma abdominalis*, and *Euchaeta norvegica* were prepared for scanning electron microscopy (SEM) and transmission electron microscopy (TEM) after the procedures of Blades and Youngbluth (1982).

SKELETO MUSCULAR SYSTEM

Descriptions at the light microscopic level of the endoskeleton and muscular systems in free-living copepods are provided by Hartog (1888) for *Cyclops*, Fahrenbach (1962) for a harpacticoid, and Lowe (1935), Perryman (1961) and Park (1966) for calanoids. Considerable information is available on the ultrastructure of copepod muscles, particularly with respect to some cyclopoids (Bouligand, 1962, 1963, 1964, 1966; Fahrenbach, 1963, 1967). Raymont and co-workers (1974) presented limited observations on the fine structure of the muscles in *Calanus finmarchicus*.

Due to the complexities of the skeleto-muscular system in copepods, general anatomical aspects and ultrastructure will be summarized here. The reader is referred to the above citations for more specific information.

Endoskeleton

The endoskeleton of many crustaceans consists of endosternites and apodemes. An endosternite is a sclerotized process on the inner surface of the cephalosomal exoskeleton and apodemes are infoldings of the procuticle that produce inner projections. Both structures provide for muscle attachment.

As summarized by Marshall and Orr (1955), the endoskeleton of *Calanus finmarchicus* consists of two tendinous ventral endosternites situated one behind the other along the midsagittal line, and by numerous cuticular apodemes (Fig. 1A). The first endosternite lies between the bases of the mandibles just posterior to the esophagus. It supports the muscles of the antennae, mandibles and first maxillae. The second endosternite lies at the level of the second maxillae and supports muscles for the first and second maxillae and maxillipedes. One pair of apodemes arises from the ventral surface, behind and lateral to the bases of the first maxillae. These provide stability to the endosternites and serve for the attachment of the large ventral longitudinal muscles of the prosome (Fig. 1B). A pair of postmaxillary apodemes arises behind and lateral to the bases of the second maxillae and extends from the ventral surface to the lateral exoskeleton. A pair of large apodemes is present in each of the metasomal segments. These attach to the couplers connecting the coxopodites of the swimming legs and are the points of attachment of the flexor muscles for these limbs. A pair of very slender chitinous ingrowths is found in each of the third, fourth and fifth metasomal segments. These pass from the ventral surface dorsolaterally across the body cavity and attach to the dorsomedial surfaces of the walls of the genital ducts, thus providing support for the ducts.

The endoskeletal configuration described above for *C. finmarchicus* is generally similar to that of *Epilabidocera amphitrites* (Park, 1966). Both calanoids have two endosternites with the same general structure but show considerable differences in their detailed anatomy. Lowe (1935) described only one pair of apodemes connected with each pair of swimming legs in *C. finmarchicus*, whereas Park (1966) reported two pairs in *E. amphitrites*.

Musculature

For calanoids in general, the musculature is divided into limb and longitudinal trunk muscles. Perryman (1961) gives the most detailed account of the skeleto-musculature of a calanoid by dealing

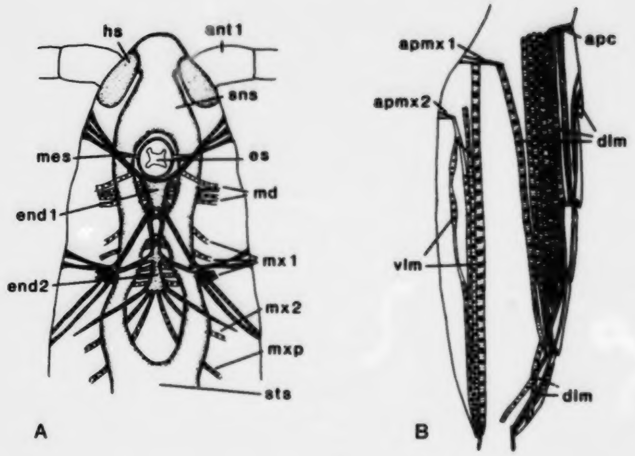


Figure 1. *Skeleto-musculature.* **A.** *Anterior body region of Calanus finmarchicus showing endosternites (end1, end2) and sinuses. Ventral view. ant1 = first antenna, es = esophagus, hs = head sinus, md = mandibular muscles, mes = muscle from endosternite to esophagus, mx1 = muscle to first maxilla, mx2 = muscle to second maxilla, mxp = muscle to maxilliped, sns = supraneural sinus, st. = sternal sinus. (Modified from Lowe, 1935)* **B.** *Longitudinal trunk musculature in Epilabidocera amphitrites, lateral view from left. apc = cervical apodeme, apmx1 = post-maxillulary apodeme, apmx 2 = post-maxillary apodeme, dlm = dorsal lateral muscles, vlm = ventral lateral muscles. (Modified from Park, 1966)*

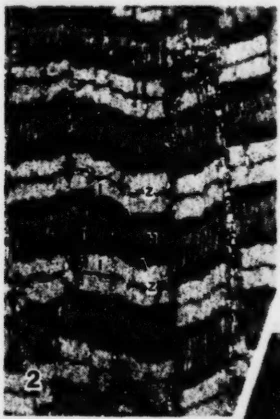


Figure 2. *Longitudinal section through longitudinal muscle in the abdomen of Labidocera aestiva. Note A and I bands, H zone and Z line. X 7,600.*

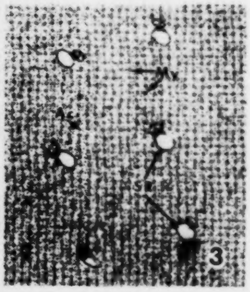


Figure 3. *Transverse section through slow muscle in Euchaeta marina showing irregular arrangement of myosin (My) and actin (Ac) filaments. SR = sarcoplasmic reticulum. X 42,200.*

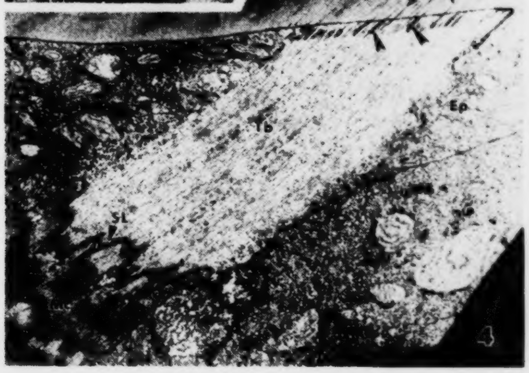


Figure 4. *Muscle attachment to cuticle (CT) in Pleuromamma abdominalis. Ep = epidermal cell, Mc = muscle, SL = sarcolemma, Tb = tonofibrils, Tf = tonofilaments. Unlabelled arrows indicate dense zones. X 6,450.*

with the head, metasomal and abdominal regions, and associated appendages individually. The musculature of the appendages is particularly complex and will not be dealt with here. The reader is referred to Perryman (1961) for details.

The musculature of the prosome consists of a pair of dorsal and a pair of ventral groups. Anteriorly, each dorsal longitudinal muscle consists of eight large muscle fibers arranged in a sheet which is closely applied to the dorsolateral exoskeleton. These extend from the level of the cervical groove and the post-maxillulary apodeme to the end of the metasome (Fig. 1B). Each ventral longitudinal muscle is composed of six fibers behind the level of the second pair of swimming legs. These extend posteriorly through the lower lateral part of the body cavity to insert on the anteroventral edge of the urosome. The longitudinal muscles of the urosome are arranged as paired dorsal, ventral, and lateral groups. These run the length of the urosome, originating at its anterior end.

Three additional pairs of slender muscles separate from the major muscle groups are also present. One pair supports the heart, extending dorsally from the first to the fourth metasomal segment. The second pair functions in the expansion and contraction of the pericardial cavity, running from the dorsal exoskeleton to the pericardial floor. The third pair is present in the wall of the genital ducts. Another group of muscles surrounds the digestive tract.

Ultrastructure of muscles

Several studies by Bouligand describe the ultrastructure of striated muscles in various species of Cyclops, including their attachments to the cuticle (1962), their membrane systems and myoneural junctions (1963), and the mechanisms of contraction (1964). Fahrenbach (1963) investigated the fine structure of the fast acting abdominal musculature of the cyclopoid Macrocyclops albidus as well as the slow muscles of the esophagus, midgut, hindgut and openings of the oviduct (1967). Briggs (1979) reported on the fine structure of the longitudinal trunk and gut muscles in the cyclopoid Parenthessius anemoniae. In general, the ultrastructure of the muscles is the same in these copepods and is comparable to that of other arthropods.

Each muscle fiber contains groups of myofibrils that consist of a regularly arranged system of thick myosin and thin actin filaments. A branching, tubular system of membranes, the sarcoplasmic reticulum, runs longitudinally through and around the myofibrils (Fig. 3). The sarcoplasmic reticular system shows an unusual elaboration in the fast muscles of the body and appendages, whereas the slow muscle fibers of the digestive and reproductive tracts have a reduced sarcoplasmic reticulum. In longitudinal section, the typical striation of skeletal muscle is seen with distinct, alternating light and dark regions that represent the A and I bands, H zone and Z line (Fig. 2). The transverse section of a fast fiber reveals the hexagonal array of myofilaments typical of arthropod muscles, in which each thick myosin filament is surrounded by six thin actin filaments. In the slow muscle fibers of copepods however, each thick filament is surrounded by approximately 12 thin filaments in no regular pattern (Fig. 3).

Nuclei of the muscle fibers are located peripherally. Mitochondria tend to be very large and are concentrated in dense layers under the sarcolemma (= plasma membrane) of each fiber. Innervating axons form synapses with the sarcolemma at frequent intervals. However, Fahrenbach (1963) reported that the neuromuscular junction is relatively unspecialized.

Muscle attachment

Muscles attach to the cuticle (Fig. 4) by means of special structures analogous to tendons and reffered to as tonofibrils (Bouligand, 1962). The tonofibrils are composed of groups of tubules (diameter of 12.5 - 15.0 nm), called tonofilaments (Bouligand, 1962). Near the attachment site of the cuticle the muscle fibrils terminate at an irregular line of sarcolemma which is attached to another plasma membrane. The tonofilaments emerge from the plasma membrane, traverse the cytoplasm of the epidermal cells which run between the muscles and the cuticle (Fig. 4), then pass in groups through electron-dense zones immediately beneath the cuticle (Fig. 4). The tonofilaments emerge from the dense zones and ramify through the cuticle forming a firm attachment.

DIGESTIVE SYSTEM

The structure of the digestive tract in free-living copepods has been described at the light microscope level for some calanoids (Dakin, 1908; Lowe, 1935; Marshall and Orr, 1955; Park, 1966; Musko, 1983), two harpacticoids (Fahrenbach, 1962; Yoshikoshi, 1975) and a fresh water cyclopoid (Musko, 1983). Considerable information is now available at the ultrastructural level for several species of calanoids (Ong and Lake, 1969; Raymont et al.,1974; Arnaud et al., 1978, 1980; Hallberg and Hirche, 1980), and one harpacticoid (Sullivan and Bisalputra, 1980). Gharagozlou-van Ginneken (1977) provides fine structural details on the labral glands of two harpacticoids.

The digestive tract consists of the mouth, esophagus, midgut and hindgut which opens at the anus in the posterior end of the urosome. This arrangement is generally consistent within the copepods studied, although variations occur in the number of midgut regions and cell types that compose the midgut epithelium.

Mouth

The reader is referred to Fahrenbach (1962) and Park (1966) for detailed descriptions of anatomy of the oral region. Depending on the species, the mouth area contains a variable number of labral glands. Eight glands have been reported in calanoids (Lowe, 1935; Park, 1966). Gharagozlou-van Ginneken (1977) described the labral glands of *Porcellidium fimbriatum* and *P. viride*, as unicellular, paired and symmetrically arranged along each side of the median line of the labrum. The glands form a secretory unit composed of three morphologically distinct cellular types. It was concluded that the labral glands of copepods exhibit classical secretory activity analogous to that of the salivary glands in certain insects (Gharagozlou-van Ginneken, 1977). Ong and Lake (1969) suggested that mucus produced by the labral glands in copepods mixes with the food as it passes into the esophagus and is probably responsible for protecting the gut from its own digestive enzymes.

Esophagus

The esophagus, sometimes called the foregut, connects the mouth and the midgut (Fig. 6). It is lined with chitin which covers a thin epithelial layer. This epithelium has no apparent secretory activity (Sullivan and Bisalputra, 1980).

Midgut

The midgut is the most extensive part of the digestive tract. It extends from the esophagus to near the end of the urosome (Fig. 5). The midgut can be divided generally into three morphological zones designated as the anterior zone I, the middle zone II, and the posterior zone III (Arnaud et al., 1978, 1980). Depending on the species, zone I extends from the esophagus to nearly the end of the cephalosome, zone II from the last third of the cephalosome to the first two metasomal segments, and zone III through the remainder of the metasome and into the urosome ending at the hindgut (Figs. 5, 10).

In many calanoids, an extension of zone I, referred to as the midgut diverticulum (Park, 1966; Arnaud et al., 1980), runs from the esophagus anteriorly into the dorsal region of the head before it proceeds posteriorly (Fig. 6). A relatively small, sac-like diverticulum was noted in the harpacticoids *Diarthrodes cystoecus* (cf. Fahrenbach, 1962), *Tigriopus japonicus* (cf. Yoshikoshi, 1975), and *Tigriopus californicus* by Sullivan and Bisalputra (1980) who referred to this area as the midgut caecum.

A variety of cell types are found throughout the three zones of the midgut. Although the nomenclature of these cell types varies in the literature, their morphological and functional characteristics are generally similar between species. The principle cellular categories are R, D, F, and B (Arnaud et al., 1980).

The R and D cells have long microvilli and contain both granular and smooth forms of endoplasmic reticulum (ER). The R cells (Fig. 7) are localized in zones I and III and appear to have an absorptive function. The narrow, dense D cells are found in zone II situated between the voluminous, vacuolar B cells. The function of the D cells is unclear. The F cells, present in zone I and II, contain abundant granular ER and phagosomes. They reportedly secrete digestive enzymes.

The vacuolar B cells (Fig. 8) are characteristic of the digestive tract of calanoids and are strictly limited to zone II (Arnaud et al., 1980). They are present in other copepods, but often in more than one zone of the midgut. Intense pinocytotic activity occurs at the base of microvilli that line the apical border of the B cells (Fig. 9). The large vacuoles within these cells are developed apparently from fusion of the many pinocytotic vesicles present in the apical cytoplasm (Fig. 9). Masses of electrondense material are present within the large vacuoles (Fig. 8).

Fahrenbach (1962) proposed an excretory function for the vacuolar cells of the harpacticoid *Diarthrodes cystoecus*. Park (1966) reported that the vacuolated cells in *Epilabidocera amphitrites* secrete a mucus-like substance which composes the peritrophic membrane. Briggs (1977) suggested that the B cells take in food material from the lumen of the gut by pinocytosis and concentrate it within their vacuoles. The undigested food is eliminated into the intestinal lumen by rupture of the apical wall of the B cells and is formed into fecal pellets. The B cells therefore appear to have both absorptive and excretory functions.

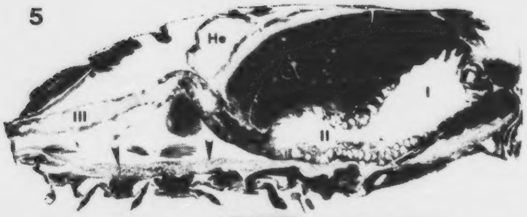


Figure 5. *Light micrograph, midsagittal section through prosome (minus head) of female Labidocera aestiva showing zones I, II, and II of midgut, ovary (OV) heart (He), and nerve cord (unlabelled arrows). View from right. X 92.*

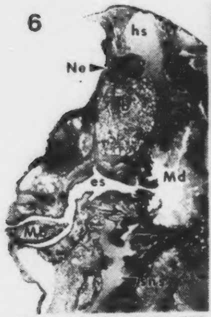


Figure 6. *Light micrograph, midsagittal section through head of Undinula vulgaris showing part of brain (b), naupliar eye (Ne), head sinus (hs), and portion of supraneural sinus (sns). Note mandibular blande (Mb) in mouth region, and chitin-lined esophagus (es) exterding from mouth to midgut diverticulum (Md). X 143.*

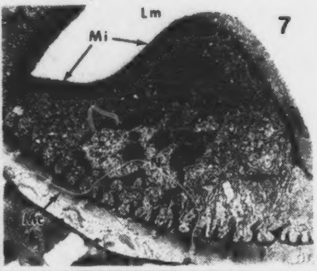


Figure 7. *Euchaeta marina. Transverse section of type R cell in zone III of midgut, second abdominal segment. Lm = lumen of gut, Mi = microvilli, Mc = muscle surrounding gut, N = nucleus. X 3,740.*

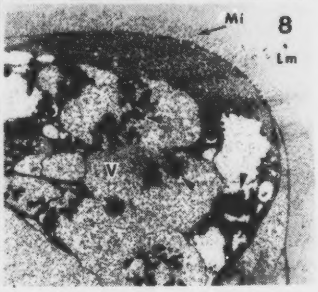


Figure 8. *Euchaeta marina, female. Transverse section of type B cell in zone II of midgut. Note large vacuoles (V) containing electron-dense masses (unlabelled arrows). Lm = lumen of gut, Mi = microvilli. X 3,350.*

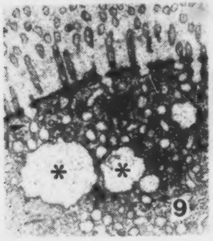


Figure 9. *Apical region of type B cell in midgut of Labidocera eastiva showing pinocytotic activity (unlabelled arrows) at - base of microvilli. * = pinocytotic vesicles. X 14,250.*

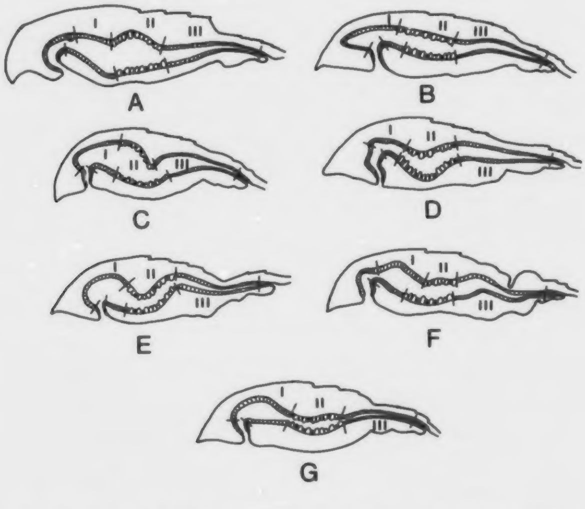


Figure 10. *Comparative morphology of the digestive system of seven calanoid copepods. I, II, and III correspond to the zones of the midgut.* **A.** *Nannocalanus minor,* **B.** *Calanus helgolandicus,* **C.** *Centropages typicus,* **D.** *Temora stylifera,* **E.** *Candacia armata,* **F.** *Labidocera wollastoni,* **G.** *Acartia clausi. (Redrawn from Arnaud et al., 1980)*

Hindgut

The hindgut is a short, weakly chitinized tube extending from zone III of the midgut through the last one or two urosomal segments to the anus. In Tigriopus californicus, the thin cuticle lining the hindgut forms many invaginations which penetrate the epithelial cells. This feature, in addition to the presence of numerous mitochondria, indicates an osmoregulatory process similar to that of insects (Sullivan and Bisalputra, 1980).

Gut musculature

The esophagus is dilated by numerous sets of muscles originating from the wall of the labrum, the general body wall, and the endosternites. Park (1966) provides details of these muscles in Epilabidocera amphitrites.

The musculature of the midgut and hindgut consists of striated circular and nonstriated fibrous longitudinal muscles. The circular muscles form a series of bands encircling the gut (Fig. 7). They are external to the longitudinal muscles and are more densely arranged in the posterior region of the midgut than in the anterior region (Yoshikoshi, 1975). Densely arranged circular muscles serve as constrictors in the anterior half of the hindgut. Dilation is accomplished by strong striated muscles which extend to the dorsal, ventral, and lateral body walls.

CIRCULATORY SYSTEM

A heart and circulatory system have not been reported in cyclopoids, harpacticoids, or in parasitic copepods (Hartog, 1888; Fahrenbach, 1962). Fahrenbach (1962) suggested that for harpacticoids, motion of the hemocoelic fluid is induced by peristalsis of the gut and by general body movements.

Lowe (1935) and Park (1966) studied the circulatory system of calanoids in great detail, describing the heart, pericardial cavity, blood sinuses and musculature. More recently, Howse et al. (1975) reported on the ultrastructure of the heart of the calanoid Anomalocera ornata, and Myklebust et al. (1977) described the ultrastructure of the membrane systems of the cardiac muscle in the calanoid Euchaeta norvegica.

The structure of the open circulatory system among calanoid species is generally the same. The heart is a thin-walled, muscular sac (Fig. 11) located beneath the dorsal body wall of the second and third, or third and fourth metasomal segments (Fig. 5). It is enclosed in a large pericardial cavity which forms the dorsal part of the body cavity in the five free metasomal segments. The anterior region of the heart tapers forward to become continuous with the narrow aorta. A bicuspid valve which prevents the backflow of hemolymph into the heart during diastole, is present at the cardio-aortic junction (Howse et al., 1975). A single slit-like ostium is present in the posterior end of the heart but does not have a valve (Fig. 11). The heart of Calanus finmarchicus (Lowe, 1935) differs slightly from that of other calanoids. It has four apertures, i.e., an anterior aorta and three venous ostia. A pair of ostia is positioned laterally in the posterior half of the heart, and a third, single ostium is ventral and posterior. The aortic valve of C. finmarchicus consists of a longitudinal slit in the floor of the heart rather than a bicuspid-type valve.

The aorta extends forward from the anterior end of the heart into the head, where it continues as the anterodorsal aortic sinus. Here it joins one or more sinuses that surround the brain and ocelli. The head sinus merges with the supraneural sinus which runs around the nerve cord in the head, bifurcates to pass around the esophagus and the endosternites, and finally opens into the perivisceral cavity (Figs. 1, 6). The perivisceral cavity forms the main cavity of the body and from it, hemolymph is returned to the pericardial cavity. Numerous smaller sinuses supply the labrum, mouth parts and the swimming legs.

There are no special respiratory organs in copepods. The exchange of gases probably takes place through sinuses or cavities that lie immediately beneath the body wall (Park, 1966).

The gross musculature of the heart is described by Lowe (1935) and Park (1966). Both circular and longitudinal muscles are present (Fig. 11). When these muscles contract simultaneously the heart contracts in all dimensions, closing the ostium and opening the aortic valve, thus forcing the hemolymph into the aorta.

The ultrastructural features of cardiac muscle cells and their membrane systems are similar in the calanoids Anomalocera ornata (cf. Howse et al., 1975) and Euchaeta norvegica (cf. Myklebust et al., 1977). A single layer of myocardial cells composes the wall of the heart (Fig. 12). Each myocardial cell contains several myofibrils that are confined to the luminal surface. The thick filaments are arranged hexagonally and each is surrounded by 8 to 12 thin filaments. Epithelial cells compose the outer surface of the heart wall. Large and abundant mitochondria are associated with the myocardial and epithelial cells (Fig. 12). The complex sarcoplasmic reticulum consists of longitudinal, oblique and transverse tubular elements. These form an intricate meshwork of interconnecting tubules that penetrate and surround each myofibril (Howse et al., 1975).

Howse et al. (1975) reported that cardiac nerves occupy deep invaginations in the myocardial cell surface and are often embedded in the peripheral sarcoplasm of the muscle cells.

EXCRETORY SYSTEM

Maxillary and antennal glands comprise the excretory system in copepods. Beyond the general descriptions provided by Lowe (1935) and Park (1966) on calanoids, and Fahrenbach (1962) on a harpacticoid, no other studies concerning these glands in copepods are available.

Both harpacticoids and calanoids have one pair of maxillary glands with basically similar morphologies. Each maxillary gland consists of three principal parts: a coelomic end-sac, a coelomic secretory tubule, and an ectodermal excretory duct (Park, 1966). The end-sac is located within, and in contact with, the lateral sinus medial to the base of the first maxilla. The wall of the end-sac is composed of a single layer of squamous epithelial cells which show no evidence of secretion. The opening between the end-sac and the tubule is guarded by a tricuspid valve that projects into the tubule thus providing one-way flow from the end-sac to the tubule.

The tubule portion of the gland is large and forms a single loop. The wall of the tubule is composed of a single layer of flat epithelial cells characterized by dense, granular cytoplasm with numerous small vacuoles, and apical microvilli. Park (1966) reported that the tubule is not in direct contact with the hemolymph, and the cells throughout the tubule are highly secretory.

The excretory duct is lined internally by a cuticle and externally by a layer of epithelial cells. It extends posteroventrally and opens to the outside on the base of the first maxilla.

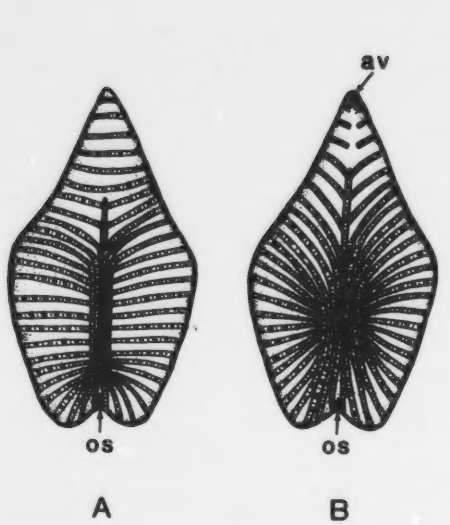


Figure 11. *Musculature of the heart wall in Epilabidocera amphitrites. A. dorsal view, B. ventral view. av = aortic valve, os = ostium. (Redrawn from Park, 1966)*

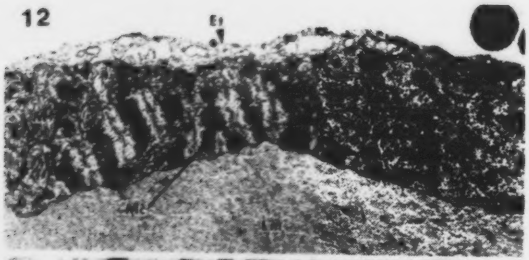


Figure 12. *Transverse section through heart wall of Labidocera aestiva showing myocardinal cells (Mc) along the luminal border and epithelial cells (Et) along the outer surface of the heart. Note numerous mitochondira (M), and lumen (Lm) of heart containing hemolymph. X 5,860.*

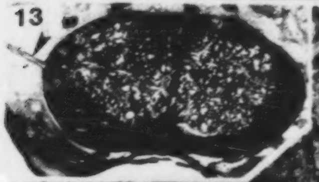


Figure 13. *Undinula vulgaris. Light micrograph, transverse section of ventral nerve cord in distal region of cephalosome. Note peripheral nuclei (N) of neurons, and nerve fiber (unlabelled arrow) leaving nerve cord. X 320.*

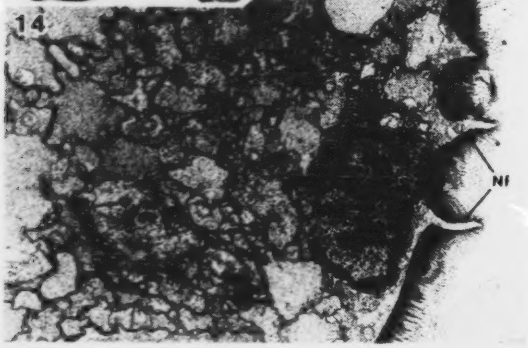


Figure 14. *Pleuromamma abdominalis. Transverse section through ventral nerve cord at level of maxillipeds. Note nerve fibers (Nf) leaving nerve cord. M = mitochondria in nerve fibers, N = nucleus of neuron. X 5,840.*

The role of each region of the maxillary gland in the excretory process has not been explained in studies on copepods. However, it is structurally comparable to that of the brine shrimp (Tyson, 1968, 1969) and presumably functions in a similar way. Tyson (1969) suggested that ultrafiltration of the blood occurs through the wall of the end-sac but not all components of the blood ultrafiltrate are retained in the final urine. The cells of the end-sac, as well as those of the tubule may resorb some of these materials. The fine structure of the excretory duct indicated that it serves primarily as a channel for the urine.

The antennal gland is the functional excretory organ of the nauplius and is not found in the adult. The antennal gland resembles a miniature of the maxillary gland but is located at the base of the antenna (Fahrenbach, 1962).

NERVOUS SYSTEM

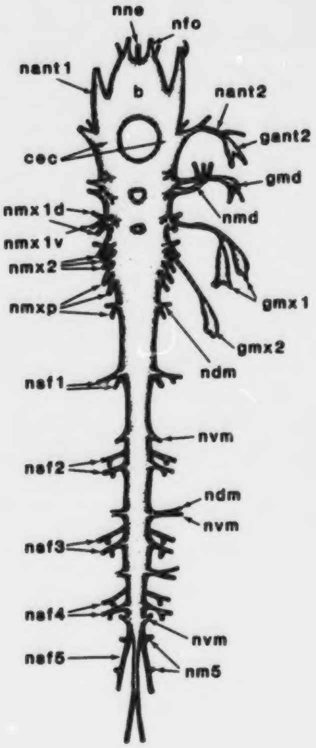
Early descriptions of the central nervous system were reported by Hartog (1888) for Cyclops, Richard (1891) for Cyclops and Diaptomus, and Hanström (1924, 1928) for Cyclops oithonides, Calanus hyperboreus, and Euchaeta norvegica. More detailed accounts were provided by Lowe (1935) for Calanus finmarchicus, Fahrenbach (1962) for Diarthrodes cystoecus and Park (1966) for Epilabidocera amphitrites. The general structure of the nervous system is similar in these copepods.

The central nervous system consists of a large brain (Figs. 6, 15) which is connected by massive circumesophageal connectives to a ventral nerve cord (Fig. 15). The brain consists of the typical protocerebral, deuterocerebral and tritocerebral lobes, although these areas are difficult to differentiate (Park, 1966). Nerves run to the eye and frontal organs from the anterior end of the brain, and other nerves to the appendages and body musculature either from the brain, the circumesophageal connectives or the ventral nerve cord.

According to Lowe (1935), the two halves of the nerve cord are fused along their entire length except for two small openings in the mandibular and maxillulary segments where muscles pass through from the endosternite to the body wall. The nerve cord (Figs. 5, 13, 14) extends to the last metasomal segment where it bifurcates into a ventral and dorsal nerve (Fig. 15). The ventral nerve supplies the fifth pair of swimming legs. The dorsal nerve divides into right and left branches that run the length of the abdomen to terminate in the caudal rami. Ganglion cells are present throughout the nerve cord and are arranged into ganglia in the metasomal segments.

Giant fiber system

Two pairs of interneurons and numerous giant motor fibers form a giant fiber system in copepods that is comparable to that of the Decapoda. The giant fiber system in copepods supplies all the muscles that are involved in the rapid escape movements, i.e., the muscles of the first antennae, the swimming legs and the dorsal longitudinal muscles. A pair of giant fibers extends along the length of the nerve cord, one on each dorsolateral surface of the cord. These fibers leave the brain anteriorly to innervate the antennules. Along the nerve cord, each giant fiber gives off branches alternately to the intersegmental and segmental nerves of the metasome. The intersegmental nerves supply the dorsal longitudinal trunk muscles and the segmental nerves run to the flexor muscles of the swimming legs. A


nne
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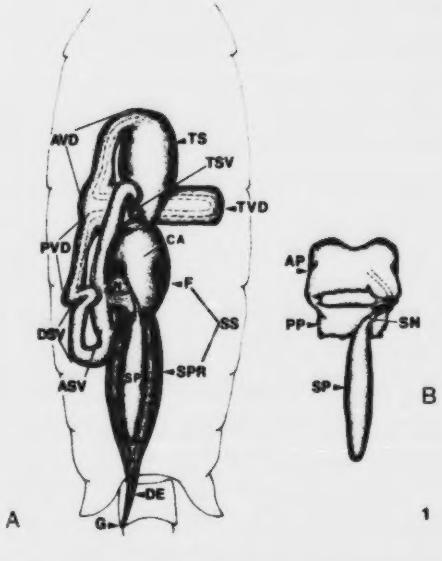
ndm
nsf1
nvm
nsf2
ndm
nvm
nsf3
nsf4
nvm
nsf5
nm5

Figure 15. *Dorsal view of central nervous system in Calanus finmarchicus showing ganglia and roots of nerves. b = brain, cec = Circumesophageal connectives, gant2 = basal ganglion of second antennal nerve, gmd = basal ganglion of mandibular nerve, gmx1 = basal ganglia of first maxilla nerves, gmx2 = basal ganglion of second maxilla nerve, nant1 = nerve to first antenna, nant2 = nerve to second antenna, ndm = giant fibers supplying dorsal longitudinal muscles, nfo = nerve to frontal organ, nmd = nerve to mandible, nm5 = nerves to muscles of fifth pair of swimming legs, nmx1d = nerves to muscles of maxillary segment, nmx1v = nerve to first maxilla, nmx2 = nerves to second maxilla, nmxp = nerves to maxillipeds, nne = nerve to nauplius eye, nsf1-5 = nerves to swimming legs, nvm = nerves to ventral longitudinal muscles. (Modified from Lowe, 1935).*

Figure 16. ***A.*** *Male reproduction system of Labidocera aestiva, dorsal view. ASV = ascending seminal vesicle, ADD = anterior ductus deferens, CA = coupling apparatus, DE = ductus ejaculatorius, DSV = descending semiral vesicle, G = gonopore, PDD = posterior ductus deferens, SN = spermatophore neck, SP = spermatophore proper. Spermatophore sac (SS) is subdivided into anterior former (F), and posterior sac proper (SPR). TDD = transverse ductus deferens, TS = testis, TSV = terminal part of seminal vesicle.* ***B.*** *Diagramatic illustration of spermatophore complex of Labidocera aestiva. AP = anterior coupling plate, PP = posterior coupling plate, SP = spermatophore proper, SN = spermatophore neck. (Modified from Blades and Youngbluth, 1981).*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B
1

single impulse in any of the giant fibers which innervate the dorsal longitudinal muscles, antennules and swimming legs is sufficient to cause the necessary complex muscular contractions that elicit the rapid escape response.

Nauplius eye

Excellent studies on the anatomy, cytology and innervation of the nauplius eye, using both light and electron microscopy, are available for a variety of copepods (Esterly, 1908; Vaissière, 1961; Fahrenbach, 1962, 1964; Park, 1966; Elofsson, 1969; Dudley, 1969; Wolken and Florida, 1969; Vaissière and Boulay, 1971).

The simple nauplius eye (Fig. 6) is composed of three tightly apposed ocelli. Each ocellus consists of a pigmented cup filled with receptor or retinula cells, which are usually fewer than ten in number. Optic nerve fibers leave the retinula cells and run to the nauplius eye-center in the protocerebrum. The above references reveal specific differences in the eyes of various copepod species.

More highly developed eyes are found in pontellids (Park, 1966), Sapphirina and Corycaeus (Elofsson, 1969), and Copilia (Wolken and Florida, 1969). In Copilia for example (Wolken and Florida, 1969), only the female possesses these advanced eyes that comprise more than half the body. Each eye appears as the single ommatidium of a compound eye with a corneal lens, crystalline cone and retinula cells that form its rhabdom. The rhabdom lies in a pigmented stem which oscillates back and forth. The authors suggest that the lens system acts as an optical "light amplifier" to increase the light collecting efficiency of the anterior lens. This form of lens system would be quite suitable for Copilia who live at depth where light levels are low.

REPRODUCTIVE SYSTEMS

Males

In the Copepoda, the presence of aflagellate, nonmotile spermatozoa and the absence of copulatory organs are compensated by the evolution of spermatophores which are produced within the highly specialized genital tract of the male. During copulation the male attaches a spermatophore on or near the gonopore of the female and the spermatozoa are subsequently transferred into subcuticular, spermathecal sacs where they are stored until the female spawns.

Spermatophores produced by the majority of copepods adhere to the female by a cement-like substance present on the open end of the flask. Some calanoids, e.g., Pontellidae and Centropagidae, produce a spermatophore that is connected to one or more chitin-like plates. These plates, referred to as the coupling apparatus (after "Koppler", Heberer, 1932a), also carry adhesive secretions and attach the spermatophore to a precise location on the urosome of the female (Blades and Youngbluth, 1979).

Male genital tract and spermatophore formation

The morphology of the male genital system and the process of spermatophore formation have been studied for a variety of copepods using light microscopy (Heberer, 1932a, 1937, 1955; Fahrenbach, 1962; Park, 1966), and electron microscopy (Raymont et al., 1974; Manier et al., 1977; Rousset et al., 1978; Coste et al., 1978; Hopkins, 1978; Gharagozlou-van Ginneken and Pochon-Masson, 1979; Blades and Youngbluth, 1981).

The reproductive tract of male calanoids consists of a single testis and a long, winding genital duct that lies sinistrally and terminates at a gonopore on the first urosomal segment. Harpacticoids reportedly have one testis and one genital duct although the duct may lie in either the right or left body cavity (Fahrenbach, 1962; Gharagozlou-van Ginneken, 1978). In the Cyclopoida there may be one testis, a testis divided by a mid-sagittal partition or 2 testes, and two genital ducts that run to paired gonopores (Rousset et al., 1981).

The following description of the male genital system and process of spermatophore formation is summarized from Blades and Youngbluth (1981) for the pontellid Labidocera aestiva. The genital duct is morphologically divided into the ductus deferens, seminal vesicle, spermatophore sac, and ductus ejaculatorius.

A single pyriform testis lies dorsal to the gut and extends longitudinally to the first matasomal segment (Figs. 16, 21). Spermatids in the broadened anterior end of the testis are released into a central lumen that merges with the ductus deferens. The wall of the ductus deferens consists of highly glandular, columnar epithelial cells that contain extensive arrays of rough ER (Fig. 17) and abundant, well-developed Golgi complexes. The anterior and central regions of the ductus deferens produce, and release into the lumen a flocculent substance and two granular secretions that constitute the seminal fluid. In its terminal part, the ductus deferens synthesizes another secretion that forms the spermatophore wall enclosing the spermatozoa and seminal fluid (Fig. 17). Development of the spermatophore wall is completed in the thin-walled seminal vesicle, although this region functions primarily as a storage organ (Fig. 18).

Joining the seminal vesicle is an elongate, highly glandular spermatophore sac (Fig. 16). The various plates of the coupling apparatus are developed in the anterior region of this sac, referred to as the "former" (after Heberer, 1932a), by secretions from eight different cell types. The posterior region of the sac, or sac proper, stores the flask-shaped spermatophore and produces secretions that aid ejaculation of the entire spermatophore complex (Fig. 19).

When the spermatophore is extruded from the male metasome during copulation, it passes from the spermatophore sac down the narrow, chitin-lined ductus ejaculatorius and exits through the gonopore which appears as a ventrolateral slit in the left posterior border of the first urosomal segment (Fig. 16). At the same time, the contents of the seminal vesicle flow into the vacant lumen of the sac proper with only minor disturbance to the concentric arrangement of spermatozoa and seminal secretions (Fig. 19). As the coupling plates leave the lumen of the former, the various cell types composing its walls begin to secrete the plates of a new coupling apparatus.

The process of spermatophore formation in Labidocera aestiva is generally similar to that of other calanoids (Park, 1966; Raymont et al., 1974; Hopkins, 1978), harpacticoids (Fahrenbach, 1962; Gharagozlou-van Ginneken and Pochon-Masson, 1979), and some parasitic copepods (Manier et al., 1977; Coste et al., 1978; Rousset et al., 1978). Interspecific differences are related to (1) the number of types of secretion granules produced by the ductus deferens, (2) the arrangement of these secretion granules in

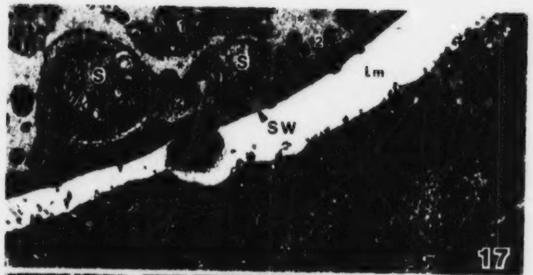

Figure 17. *Luminal border of transverse ductus deferens in Labidocera aestiva. Note variuos granular (1, 2) and flocculent (*) secretions surrounding spermatids (S) in the developing spermatophore. ER = endoplasmatic reticulum composing cells of ductus deferens, Lm = lumen, N = nucleus, SW = developing spermatophore wall. X 6,460 (From Blades and Youngbluth, 1981).*

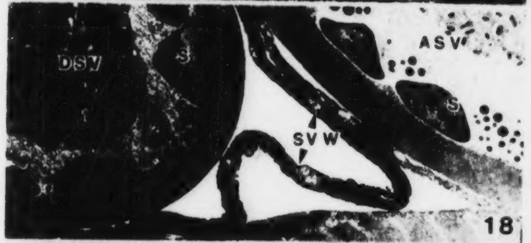

Figure 18. *Transverse section through descending seminal vesicle (DSV) and ascending seminal vesicle (ASV) in Labidocera eastiva. Note that spermatophore wall (SW) is fully developed in ascending seminal vesicles. Seminal fluid that accompanies spermatozoa consists of flocculent material (*) and two types of granules (1, 2). SVW = wall of seminal vesicle. X 4,300. (From Blades and Youngbluth, 1981).*

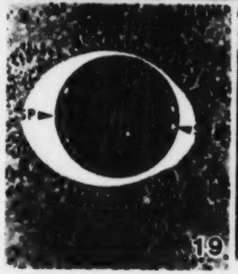

Figure 19. *Light micrograph, transverse section through anterior part of spermatophore sac proper in Labidocera aestiva. Mature spermatophore (SP) in lumen. Note arrengement of spermatozoa (S) and seminal secretion (*). Dark bodies in epithelial cells of spermatophore sac are secretory vesicles. X 760. (From Blades and Youngbluth, 1981).*

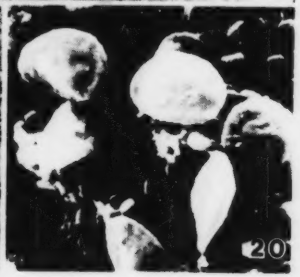

Figure 20. *SEM showing disk-shaped, flattened spermatozoa (S) from ripe spermatophore of Lobidocera aestiva. X 6,860. (From Blades and Youngbluth, 1982).*

the spermatophore with respect to the spermatozoa, (3) the number of secretions composing the spermatophore wall and, (4) the presence or absence of a well-developed former.

From light microscopic examinations of a variety of calanoid copepods, Heberer (1932a) proposed a phylogenetic scheme based on the gross morphology of the mature spermatophore and on the organization of the male genital system, particularly the structure of the former. According to this scheme, the simple type of former, as found in Euchaeta norvegica (Hopkins, 1978), represents a primitive condition. From this simple former, a highly complex of glands has evolved within the male. These glands produce the numerous secretions which form the intricate plates of the coupling apparatus. Members of the Pontellidae and Centropagidae are particularly known for possessing highly derived formers.

Spermatogenesis

The studies of Heberer (1924, 1932b), Fahrenbach (1962) and Park (1966) provide descriptions of spermatogenesis at the light microscope level, but ultrastructural accounts of spermatogenesis are available for only two species of harpacticoids (Pochon-Masson and Gharagozlou-van Ginneken, 1977; Manier et al., 1977), one cyclopoid (Rousset et al., 1981), and a calanoid (Blades-Eckelbarger and Youngbluth, 1982). Certain fine structural features of the late spermatids and mature spermatozoa of Cyclops sp. were examined more recently by Reger and Fitzgerald (1983).

The presence of two morphological types of fertilizing spermatozoa has been noted in the Copepoda: those that are ovoid or disc-shaped (Calanoida and Cyclopoida), and others that are elongate or filiform (Harpacticoida). Both types are aflagellate. An acrosome has been described in the filiform spermatozoa of two harpacticoids (Fahrenbach, 1962; Pochon-Masson and Gharagozlou-van Ginneken, 1977) and Cyclops sp. (Reger and Fitzgerald, 1983) but not in the ovoid or disc-shaped spermatozoa of other cyclopoids (Manier et al., 1977; Rousset et al., 1981) and some calanoids (Park, 1966; Brown, 1966; Hopkins, 1978; Blades-Eckelbarger and Youngbluth, 1982). The following discussion will describe the events of spermatogenesis in Labidocera aestiva (Blades-Eckelbarger and Youngbluth, 1982), a calanoid possessing disc-shaped spermatozoa (Fig. 20).

All stages of spermatogenesis can be observed in a single sagittal section of the testis (Fig. 21). Spermatogonia in the process of mitotic multiplication occupy the narrow posterior end of the testis. Anterior to this, a zone of primary spermatocytes in first meiotic prophase is followed by a region of secondary spermatocytes in various stages of the second meiotic division.

The leptotene primary spermatocytes are characterized by large nuclei that contain a single nucleolus and patches of darkly staining condensed chromatin (Fig. 22). The cytoplasm contains free ribosomes and numerous elongate mitochondria. Golgi complexes and ER are rarely seen. Zygotene/pachytene primary spermatocytes are recognized by further condensation of nuclear chromatin (Fig. 23). The diplotene stage is distinguished by a homogeneous granular nucleus and a single, prominent nucleolus that lies along the inner aspect of the nuclear envelope. Synaptonemal complexes and polycomplexes are regularly seen in the nuclei of spermatocytes in the zygotene to diplotene stages (Fig. 23).

The zone of the testis adjacent and anterior to the diplotene primary spermatocytes is occupied by secondary spermatocytes in metaphase, anaphase and telophase of the second meiotic division. First meiotic metaphase, anaphase and telophase were never observed. Open and closed intercellular bridges,

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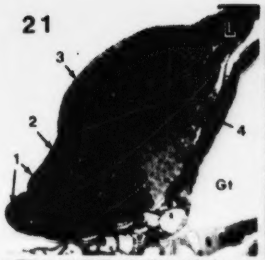

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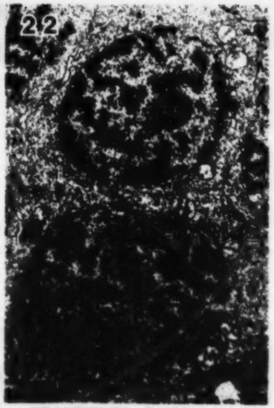

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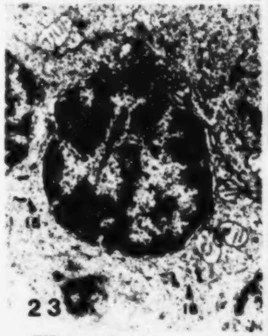

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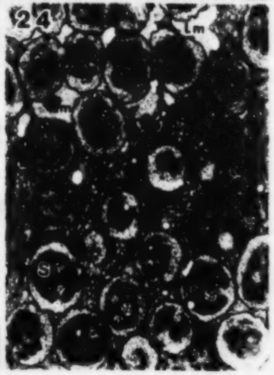

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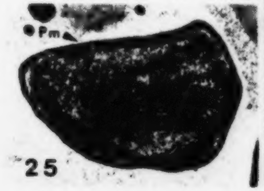

Figure 21. Light micrograph, midsagittal section of testis in Labidocera aestiva showing spermatogenic zones. Posterior end is mitotic multiplication zone (1) with spermatogonia and leptotene - primary spermatocystes. Anterior to this are meiotic zones with zygotene/pachytene (2), and diplotene (3) primary spermatocystes. Spermatids enter accessory cells in zone (4) and are released into central lumen (Lm) that joins ductus deferens. Gt = midgut. X 540. (From Blades and Youngbluth, 1982).

Figure 22. Labidocera aestiva. Two leptotene primary spermatocystes joined by open intercellular bridge (IB). M = mitochondria, N = nucleus, Nu = nucleolus. X 8,500. (From Blades and Youngbluth, 1982).

Figure 23. Labidocera aestiva. Zygotene/Pachytene primary spermatocyte showing synaptonemal poly complex (PC) in nucleus (N). IB = intracellular bridges, M = mitochoindria. X 9,895. (From Blades and Youngbluth, 1982).

Figure 24. Anterior zone of Labidocera aestiva. Accessory cells contain numerous spermatids (S), large nuclei (N) and endoplasmic reticulum (ER). Note spermatids (S*) being released into lumen (Lm) containing flocculent material. X 3,600. (From Blades and Youngbluth, 1982).

Figure 25. Spermatid in seminal vesicle of Labidocera aestiva showing nuclear envelope-derived membrane complex (unlabelled arrows) and mitochondria (M). Note electron dense material on inner and outer surface of plasma membrane (Pm). X 13,670. (From Blades and Youngbluth, 1982).

formed as a result of incomplete cytokinesis, connect the germ cells throughout spermatogenesis (Figs. 22, 23).

At the end of cytokinesis of telophase II, the young spermatids (diameter ca 5 μm) become spherical in shape, intercellular bridges disappear, and the spermatids become incorporated into large secretory accessory cells (Fig 24). These accessory cells produce a flocculent material that is released into the lumen of the ductus deferens along with the spermatids. This material forms the core of the spermatophore. Upon copulation, the flocculent material accompanies the spermatozoa into the spermathecae of the female, suggesting a possible nutritive function. Phagocytosis of spermatids is also very evident in the accessory cells. This mechanism may act to regulate the production of spermatozoa during long periods between copulations, thus preventing a build up of spermatids in the ductus deferens and seminal vesicle.

Spermiogenesis in Labidocera aestiva is less complex than that of other metazoans since neither an acrosome nor a flagellum are differentiated. During spermiogenesis the mitochondria become closely applied to the nuclear envelope, the nuclear envelope fragments and forms an elaborate membrane complex, a pentalaminar plasma membrane develops, and electron-dense material accumulates on the inner and outer surfaces of the plasma membrane of the mature spermatozoon (Fig. 25).

Mitochondria are the most numerous and prominent organelles in the spermatozoa of L. aestiva. They are present in close association with the nuclear envelope in the early stages of differentiation and later with the nuclear envelope-derived membrane complexes of the mature spermatozoon (Fig. 25). Since the spermatozoa of L. aestiva do not have a typical mitochondrial midpiece, it has been suggested that the role of the mitochondria is related to energy conservation for the prolonged metabolic maintenance of these cells.

Females

Light microscopic studies of the female reproductive system and the stages of oogenesis are available for only three species of calanoids, Eucalanus elongatus (cf. Heberer, 1930), Calanus finmarchicus (cf. Hilton, 1931; Lowe, 1935) and Epilabidocera amphitrites (cf. Park, 1966). General aspects of the female genital system were reported for Cyclops by Hartog (1888) and later for Diarthrodes cystoecus (Harpacticoida) by Fahrenbach (1962). Raymont et al. (1974) described the fine structure of previtellogenic oocytes in Calanus finmarchicus, but ultrastructural details of oogenesis and yolk formation were not defined until recently by Blades-Eckelbarger and Youngbluth (1984) for Labidocera aestiva. This work will be summarized here.

Female reproductive system

The female reproductive system of Labidocera aestiva consists of a single ovary and paired oviducts (Fig. 26). The pear-shaped ovary lies dorsal to the gut, running from posterior to anterior along the mid-axis of the the first metasomal segment. Two oviducts emerge at the proximal end of the ovary. These run anteriorly at first, then turn ventrally and extend posteriorly along either side of the gut. Each oviduct gives off intersegmentally four diverticula that extend to the ventral and lateral exoskeleton and occupy the whole space between the segmental muscles. The oviducts converge in the

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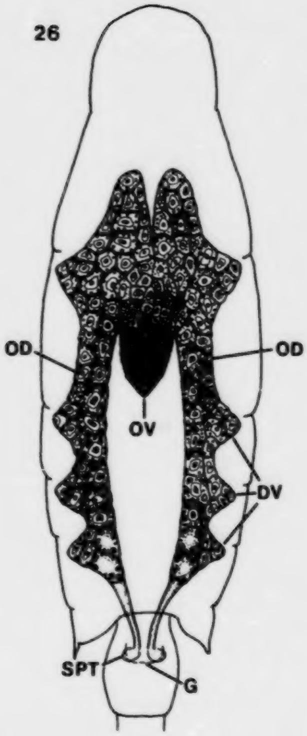

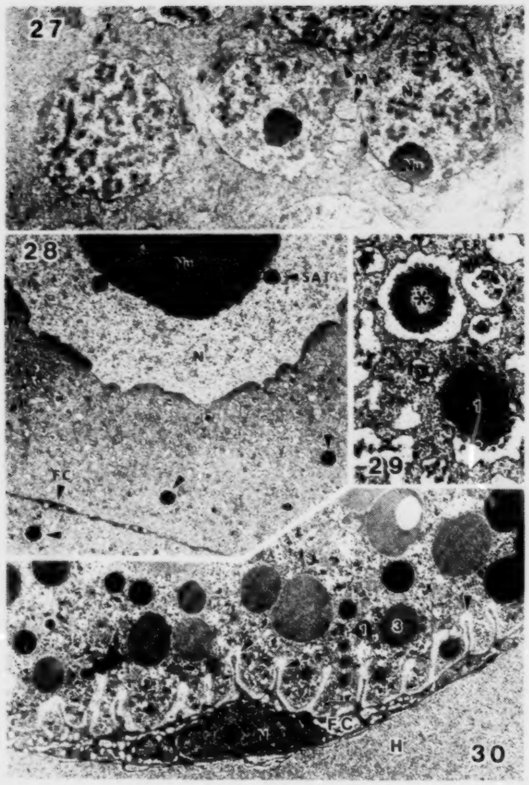

Figure **26.** *Female reproductive system of* *Labidocera aestiva, dorsal view. DV = diverticula, G = gonopore, OD = oviduct, OV = ovary, SPT = spermatheca (one of pair). (From Blades-Eckelbarger and Youngbluth, 1984).*

Figure **27.** *Zygotene/pachytene primary oocytes from Labidocera aestiva. M = mitochondria, N = nucleus, Nu = nucleolus. X 5,430.*

Figure **28.** *Labidocera aestiva. Diplotene oocyte after growth period and in early stage of type 1 yolk formation. Nucleus (N) contains large nucleolus (Nu) and nucleolar satellites (SAT). Note arrow follicle cell. Unlabelled arrows indicate developing type 1 yolk sphere. X 4,560. (From Blades-Eckelbarger and Youngbluth, 1984).*

Figure **29.** *Type 1 yolk formation in Labidocera aestiva. Fusion of electrondense granules (*) in cisternae of endoplasmic reticulum (ER). X 22,500. (From Blades-Eckelbarger and Youngbluth, 1984).*

Figure **30.** *Labidocera aestiva. Oocyte-follicle cell (FC) relationship in advanced vitellogenic stage during type 3 yolk formation. Note interdigitations (unlabelled arrows) at oocyte-follicle cell border. H = hemolyph; N = nucleus of follicle cell. X 5,700. (From Blades-Eckelbarger and Youngbluth, 1984).*

genital segment at a common gonopore. This cavity is connected also to paired spermathecal sacs (Fig. 26).

Oogenesis and yolk formation

Development of the oocytes is a continuous process and all stages of previtellogenesis and vitellogenesis can be observed in a single female. Sagittal sections through the ovary reveal the previtellogenic stages, ranging from oogonia undergoing mitotic multiplication in the narrow posterior end of the ovary, to primary oocytes in the early stages of meiotic prophase. All stages of yolk formation can be observed throughout the length of the oviducts with the early vitellogenic stages present in the anterior region of the ovary as well as the outermost part of the diverticula, and advanced stages present in the main tract of the oviducts.

Previtellogenic oocytes

The leptotene primary oocytes have an approximate diameter of 10 µm and are characterized by granular ooplasm with free ribosomes, numerous mitochondria, and a large nucleus (diameter ca. 7.5 µm). The nucleus contains a peripheral nucleolus and scattered masses of condensed chromatin. Primary oocytes in zygotene and pachytene stages (Fig. 27) are distinguished by the presence of synaptonemal complexes and polycomplexes. The diplotene primary oocytes measure approximately 20 µm in diameter with a nuclear diameter of 15 µm. Within the nucleus the chromatin masses have dispersed giving the nucleoplasm a homogeneous granular appearance. The oocytes undergo a period of growth up to the onset of vitellogenesis and remain in first meiotic diplotene throughout vitellogenesis.

Vitellogenic oocytes

The events of yolk formation are summarized in Figure 34. Three morphologically distinct forms of endogenous yolk are formed in the early vitellogenic stages. At the beginning of yolk formation (Fig. 28), the oocytes have doubled or tripled in size and are characterized by dense cytoplasm, numerous mitochondria, and a large nucleus (diameter ca. 25 µm). The nucleus contains a large nucleolus and several nucleolar satellites. The nuclear envelope is involved with intense production of vesicular and lamellar forms of ER that contain several electron-dense intracisternal granules. The fusion of these dense granules within the ER cisternae, results in type 1 yolk spheres (Fig. 29). A granular form of type 1 yolk, in which the intracisternal granules do not fuse but remain distinct within the ER (Fig. 33), appears to be synthesized by the combined activity of the ER and Golgi complexes. In the later stage of type 1 yolk formation, numerous large vesicles appear in the ooplasm that subsequently become filled with a moderately dense material. These ultimately form type 2 yolk bodies. However, the mechanism of type 2 yolk formation could not be attributed to any particular oocytic organelle and remains unknown.

A single layer of flattened follicle cells partially surrounds the oocytes in the early stage of type 1 and type 2 yolk formation (Fig. 28). In the later stages, however, the follicle cells increase in width,

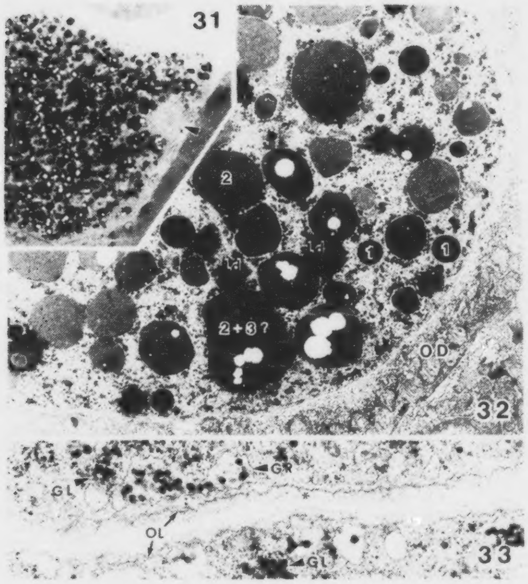

Figure 31. *Labidocera aestiva. Light micrograph, transverse section of mature oocyte prior to spawning, showing metaphase nucleus (unlabelled arrows). X 693. (From Blades and Youngbluth, 1984).*

Figure 32. *Portion of mature oocyte from Labidocera aestiva fixed as it passed through oviduct (OD) of genital segment during spawning. Note type 1 yolk spheres, type 2 (or 2 + 3?) yolk bodies, and lipid droplets (Ld). X 4,400. (From Blades and Youngbluth, 1984).*

Figure 33. *High magnification of oolemmae (OL) and flocculent egg coat (*) of two adjacent oocytes from Labidocera aestiva. Note glycogen particles (Gl) and granular form of type 1 yolk (GR). X 22,170. (From Blades and Youngbluth, 1984).*

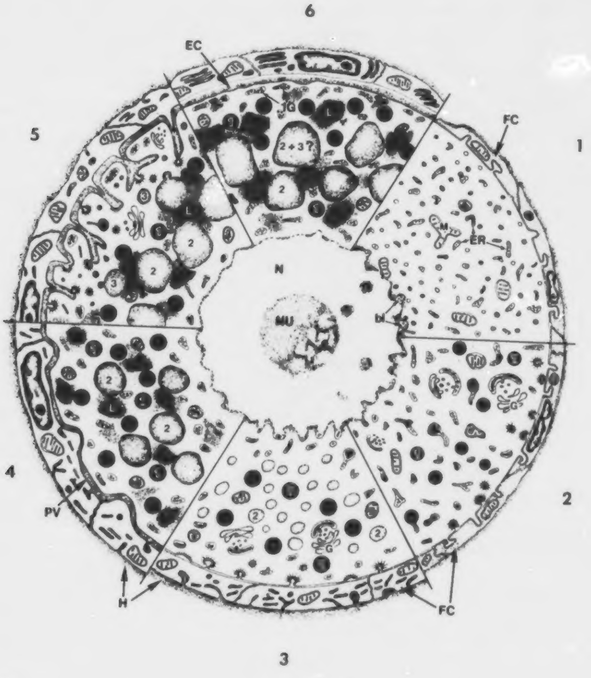

Figure 34. *Diagrammatic illustration summarizing vitellogenesis in oocytes of Labidocera aestiva. bl = blebs off of nuclear envelope, EC = egg coat, ER = endoplasmic reticulum, FC = follicle cell, G = Golgi complex, H = hemolymphe, L = lipid droplet, M = mitochondrion, N = nucleus of oocyte, NU = nucleolus, 1G = granular form of type 1 yolk. Small numbers indicate yolk types. (From Blades-Eckelbarger and Youngbluth, 1984).*

contain large nuclei and numerous mitochondria, and become filled with tubular cisternae that contain an electron-dense flocculent material. The ultrastructural evidence suggests that this material is taken up into the follicle cells from the adjacent hemolymph and released into the perivitelline space. This same material appears to compose the simple egg envelope (Fig. 33).

A heterosynthetically derived yolk is formed in the advanced stage of vitellogenesis. At this time the oolemma becomes highly infolded and interdigitates with the follicle cells (Fig. 30). Intense micropinocytotic activity occurs along the oolemma with apparent uptake of the flocculent material from the perivitelline space. Pinocytotic vesicles in the cortical ooplasm resulting from this activity, ultimately fuse with each other, or possibly with the type 2 yolk bodies, to form a third yolk type.

Prior to spawning, the nuclei of the oocytes pass from diplotene to metaphase of the first meiotic division (Fig. 31). The ooplasm of the mature oocytes contains type 1 yolk spheres, the granular form of type 1 yolk (Fig. 33) and larger yolk bodies that could be type 2 yolk or a mixture of type 2 and the heterosynthetically derived yolk (Fig. 32). Numerous lipid droplets (Fig. 32) and glycogen particles (Fig. 33) are present also. When spawned, the eggs measure approximately 90 μm in diameter.

The gross morphology of the female reproductive system of Labidocera aestiva is basically similar to that of other free-living copepods. However, due to the absence of ultrastructural studies, it is presently impossible to make comparisons of yolk formation with other copepod species. Nevertheless, some general differences can be noted at the light microscope level. According to Hilton (1931) for Calanus finmarchicus, and Park (1966) for Epilabidocera amphitrites, yolk granules are formed as intramitochondrial inclusions or in close association with the mitochondria. Mitochondria are present in large numbers in the oocytes of L. aestiva, but do not participate directly in yolk formation. Type 2 yolk and lipid droplets in the oocytes of L. aestiva are also present in the oocytes of E. amphitrites (Park, 1966), but neither Hilton (1931) for C. finmarchicus, nor Park (1966) for E. amphitrites, reported the presence of follicle cells or the appearance of a third type of yolk.

Yolk formation in the oocytes of Labidocera aestiva is very similar to that of other crustacean groups in that both autosynthetic and heterosynthetic processes are involved. However, in contrast to other crustaceans where one type of endogenous yolk is synthesized within the oocyte, three morphologically distinct types of yolk are produced by the oocytes of L. aestiva. The uptake of extra-oocytic precursors by intensive micropinocytotic activity in the advanced vitellogenic oocytes of L. aestiva generally parallels that of most other crustaceans.

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ASPECTS OF THE APPENDAGES IN DEVELOPMENT

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Abstract: Considerations are made on the morphology of the appendages, their muscle system and their function in the calanoid, cyclopoid and harpacticoid nauplii. The changes observed in their morphology and function in the copepodids are mentioned.

INTRODUCTION

From the perusal of the older authors (Gurney, 1931; Lang, 1948) and of the latest literature (Von Vaupel Klein, 1984) on appendages of copepods there are several problems related to this subject which are still to be solved and some still to be proposed. Among the latter there is the question of the origin of the first nauplius. Among the others there are the following: 1) the primitive number of podomeres on the appendages; 2) the question of which of the three orders, Cyclopoida, Harpacticoida or Calanoida, is the oldest; 3) the function of the appendages during the feeding process; 4) the most adequate nomenclature for each of the appendages and their respective parts. Some of these questions shall be discussed elsewhere during this Conference. The others, when pertinent, shall be commented upon here.

ON THE ORIGIN OF THE FIRST NAUPLIUS

Arthropodization started to exist when a trochophora-like larva acquired the capacity of producing an external carapace composed of a chitin-like material (Fig. 1). The first three pairs of jointed appendages of this nauplius-like larva appeared when the two pre-oral tentacles and the two first pairs of parapodia, produced by the posterior metamerisation of the larva, secreted the external covering of chitin-like material. The continuous movement of these appendages backwards and forwards, or up and down (Fig. 1b) may have insured at the point of flexure the development of a less rigid skeleton, and, thus, an articulation between the basis of the appendages and the body. Perhaps, by the same process or by undulating movements other articulations were maintained along the appendages, permitting motion.

Present day copepod nauplii show these same three pairs of functional limbs: the antennules, the antennae and the mandibles. The primordia of the other pairs of limbs, from maxillules to the second pair of legs, are present in the sixth naupliar stage, but, they are not functional (Fig. 2).

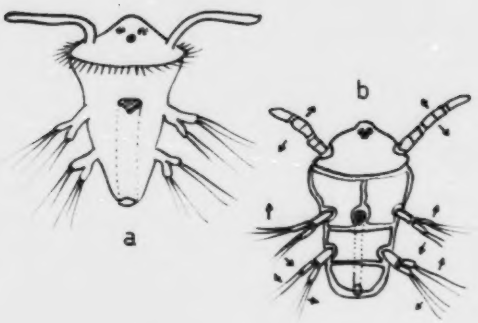


Figure 1. ***a.*** *Trochophora-like larva;* ***b.*** *The primitive nauplius, resulting from the arthropodization of a trochophora-like larva.*

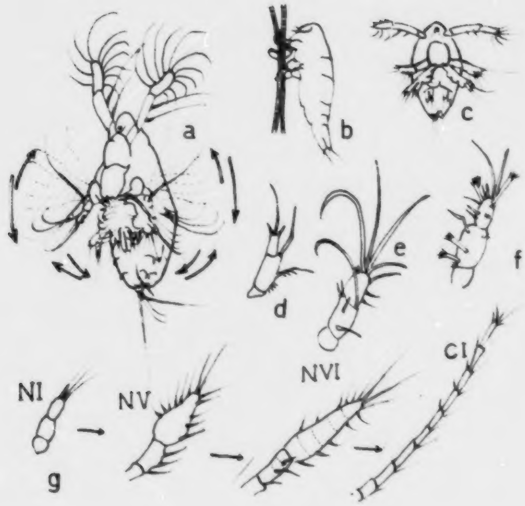


Figure 2. *The naupliar (NI,NV,NVI) and copepodid (CI) antennules:* ***a.*** *Eucalanus pileatus, the grazing nauplius, with antennules acting as keels;* ***b.*** *Macrosetella gracilis, with antennules hardly moving, because the nauplius is almost sedentary;* ***c.*** *Eucalanus nauplius (schematic) with antennule acting as a suspension organ;* ***d, e, f.*** *harpacticoid naupliar antennules with spines, spine-like and brush-ended setae (d after Gurney, 1931;* ***e*** *and* ***f*** *after Carter and Bradford, 1972);* ***g.*** *the changes undergone by the antennule from nauplius I to copepodid I in a calanoid copepod.*

THE ANTENNULES, THE ANTENNAE AND THE MANDIBLES

The antennules

They usually are three-jointed in the nauplius, but they may be one- or five-jointed, and they are always uniramous (Fig. 2). Besides specific characteristics they show others which vary with the naupliar stage and the general features of the order they belong to.

Their first function is locomotive. By moving backwards and forwards with paddle-like jerks, they pull the nauplius forwards. In some nauplii (Miracia, Macrosetella) they do not move or move very little, because the nauplius is almost sedentary. In other nauplii (Eucalanus pileatus) they act as keels, as they are maintained stretched out above the front of the nauplius, with their setae disposed fan-like around the last joint. In this case they may also aid in the suspension of the larva, when at right angles to the body (Fig. 2a, c).

At all stages of development they must have sensory functions, but studies of pores and sensillae in nauplii are unknown to me and should be investigated.

In some harpacticoids it is probable that the spines, the spine-like and the brush-ended setae of the naupliar antennule act as anchors for the larva living on algae or moss (Fig. 2d, e, f).

The first nauplius in Calanoida, Cyclopoida and Harpacticoida usually has cylindrical antennules. In Calanoida the last podomere of the antennule flattens out and becomes more paddle-shaped, with gradual addition of setae to the three terminal ones, as the nauplius grows older (Fig. 2g). The cyclopoid and harpacticoid antennule usually remains cylindrical throughout the naupliar stages. To the three terminal setae of the first naupliar stage other setae are added laterally. In the Harpacticoida instead of setae, spines or brush-like setae may appear. In the last (sixth) naupliar stage, when metamorphosis is about to take place, it is possible to see through the chitin of the last podomere of the antennule, the series of podomeres which will form the antennule of the copepodid (Fig. 2g).

The first podomere usually remains the same in the copepodid while the second is subdivided into two or three podomeres in the Calanoida and in the Cyclopoida (for more details consult Dietrich, 1915; and Oberg, 1906).

The copepodid antennule, when fully distended, is not only a suspension organ in the Calanoida, but, mostly a sensory organ for food, gravity and predators (Strickler, 1982). It generally has aesthetes and other sensors (see Saraswathy and Bradford, 1980; Von Vaupel Klein, 1984). In Harpacticoida and Cyclopoida it only rarely acts as a suspension organ in planktonic species such as Oithona. It takes part in locomotion, according to Strickler (1975) in the Cyclopoida, by beating backwards and causing the copepod to start its "jump" forwards. All harpacticoid antennules have at least one aesthete (Lang, 1948) besides other setae probably sensory. In benthic specimens the antennule also helps in anchoring the copepod to the substratum. This same function was observed in some Calanoida (Pseudodiaptomus) in which the glandular setae of the antennule "glue" these appendages to the bottom and aid the animal in forming a feeding basket with its other limbs into which food is sucked by the movement of the buccal appendages (Fig. 3d, e, f). In some Calanoida, in some Cyclopoida and in most Harpacticoida one or both of the male antennules act as grasping organs during copulation. The differentiation of the antennules into the future female and male can be observed as early as in the fourth copepodid stage in the Calanoida. In the adult the antennules are then geniculated by fusion of some podomeres. Fusion is also observed in the antennular podomeres when there is no geniculation and the fused parts may be different in the male and in the female of the same species. Within the

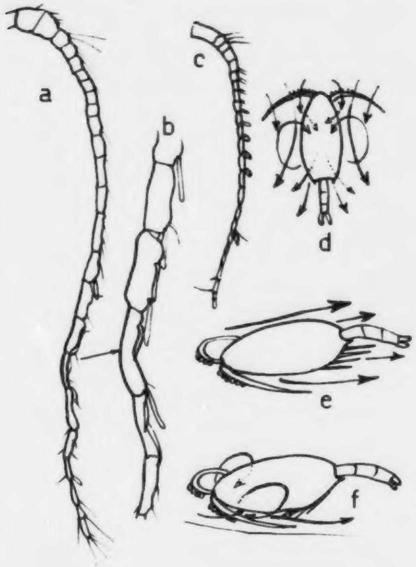


Figure 3. *The copepodid antennule:* ***a.*** *(with detail in* ***b****) geniculate antennule of male* *Bathycalanus;* ***c.*** *non geniculate antennule of* *Bradycalanus* *male;* ***d.*** *Schematic representation of* *Pseudodiaptomus acutus* *with antennules glued to the substratum, and movement of feeding currents represented by arrows (seen in dorsal view) with legs forwards;* ***e.*** *the same, seen laterally, with legs stretched out backwards;* ***f.*** *the same seen laterally with feeding basket formed by legs and oral appendages*

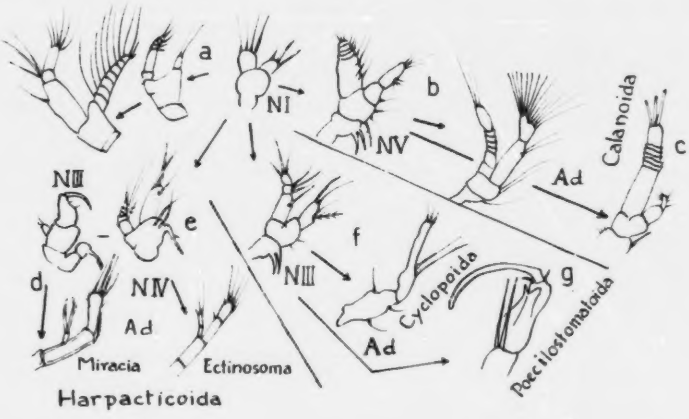

a
NI
b
NV
Calanoida
c
Ad
NIII
e
d
NIV
Ad
Miracia
Ectinosoma
Harpacticoida
NIII
f
Cyclopoida
g
Ad
Poecilostomatoida

Figure 4. *Antenna - The development of the antenna from the naupliar (N) stages to the adults (Ad.):* ***a.*** *canuellid naupliar (one-jointed endopod) antenna which metamorphoses into a copepodid antenna with a three-jointed endopod;* ***b.*** *the development of the Calanoida antenna from nauplius I (NI) through nauplius V (NV) to adult Calanid and* *Pseudochirella* *antenna (****c****);* ***d.*** *Miracia* *antenna of nauplius III and the adult antenna;* ***e.*** *Ectinosomid antenna of nauplius IV and the adult antenna;* ***f.*** *Antenna of* *Oithona* *nauplius III and of the adult;* ***g.*** *antenna of adult* *Corycaeus.* *(Antenna of* *Pseudochirella* *taken from Von Vaupel Klein, 1984).*

same family (Megacalanidae) there may be genera with and others without geniculation of the male antennule (Fig. 3a, b, c).

The antennae

The antennae are biramous in all nauplii of copepods studied up to now. They usually have a flat coxopod, which is provided with spines or setae or a blade-like projection aiding in pushing the food into the mouth. The basipod also has spines or setae and sometimes an endite with food pushing functions. The exopod generally is 2- to 5-jointed, but there are exopods with up to 10 podomeres. The exopod is locomotive. The endopod usually is one-jointed, sometimes two-jointed. The endopod of Longipedia and Canuellidae nauplii, the most primitive harpacticoid nauplii according to Lang (1948), is one-jointed, whereas in the adult it is three-jointed. This could be used as proof that the evolution can be accelerated in the nauplius and retarded in the adult. The endopod is ornamented with setae and sometimes spines or spinules. In the Harpacticoida it may have a terminal spine or hook (Fig. 4d) and is capable of hooking on to the substratum. Longipedia and Microsetella, planktonic harpacticoid nauplii, do not display this hook-like structure and are provided with simple plumose setae, like the other planktonic nauplii of the Cyclopoida and Calanoida (Fig. 4a, e).

During metamorphosis the basipod of the antenna suffers a small regression and sometimes the endopod is also reduced (e.g. Euchirella, Fig. 4c). In many copepodids there is a partial or even a total reduction of the exopod (as in Euaugaptilus and Oithona, respectively; Fig. 4f). In the last case the antenna becomes uniramous. In Corycaeus (Fig. 4g) it changes into a powerful grasping organ, less accentuated in other genera such as Oncaea. In the male Corycaeus this organ is used for holding the female, during copulation. In many Calanoida the biramous antenna has an important role in the gliding movement of the copepodid while grazing (Gauld, 1966). In the harpacticoid Miracia, from a grasping organ in the nauplius it changes into a simple setuled antenna with a very reduced exopod in the copepodid, and is then a suspension organ with possible sensory activities. A detailed comparative study of the reduction of the exopod of the antenna in the harpacticoids is found in Lang (1948).

The mandible

It is also biramous in all the first naupliar stages (Fig. 5a). In the orthonauplii (nauplius I and II) and usually in the first metanauplius (nauplius III) it is composed of a coxopod or coxa, a basipod, an endopod and an exopod. The coxopod has a spine or seta, which in the second and/or third metanauplius of the Calanoida changes into a mandibular blade (Fig. 5b) or into the rudiments of the gnathobase. The coxa of the Cyclopoida and of the Harpacticoida may be differently ornamented, but, it has no such blade or rudiment in the nauplius (Fig. 5c). In the majority of species a gnathobase only appears after metamorphosis.

The exopod usually is four- or five-jointed in the Calanoida nauplii and four-jointed or less, even one-jointed due to fusion of podomeres, in the Harpacticoida and Cyclopoida. The mandibular endopod is one-jointed in the Calanoida and alsp in the Harpacticoida (Fig. 5b, e), with the exception of Longipedia and Sunaristes (Canuellidae) where it is two-jointed. This is also the case in all the nauplii of the Cyclopoida (Fig. 5d) and of their nearest of kin, the free-living, parasitic and commensal

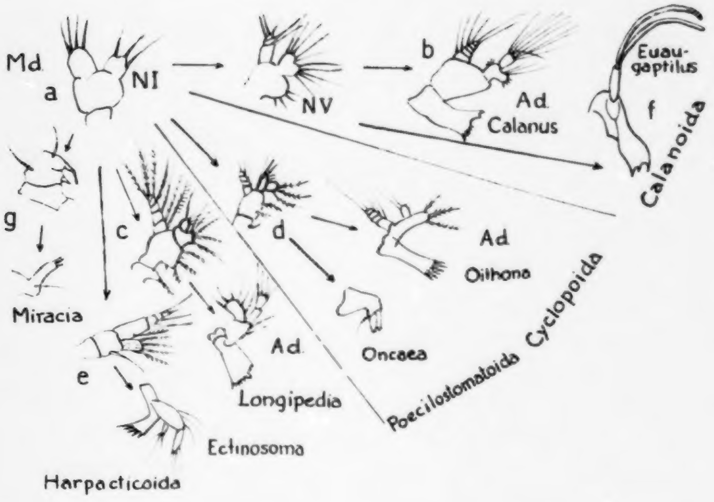
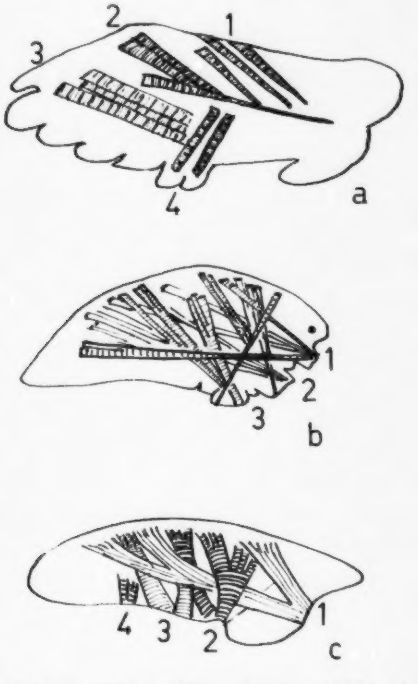

Md
a
NI
NV
b
Ad
Calanus
Euaugaptilus
f
Calanoida
g
c
d
Ad
Oithona
Cyclopoida
Miracia
Ad
Oncaea
Poecilostomatoida
e
Longipedia
Ectinosoma
Harpacticoida

Figure 5. *Mandibles:* ***a.*** *Mandible of nauplius I (NI), nauplius V (NV) metamorphosing into* ***b.*** *adult (Ad.) mandible of Calanus and of Euaugaptilus* ***(f)****;* ***c.*** *mandible of Longipedia (with two-jointed endopod) in the nauplius and in the adult (Ad.);* ***d.*** *mandible of Oithona nauplius and of adult (Ad.), also with double-jointed endopod; the Oncaea mandible (copepodid);* ***e.*** *Ectinosomid mandible in the nauplius and in the adult;* ***f.*** *Euaugaptilus mandible (adult);* ***g.*** *Miracia mandible with hooks in the nauplius and in the adult without hooks.*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2
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c

Figure 6. *The muscle system of the nauplii (from Fanta, 1972a, b):* ***a.*** *Oithona simple muscles, nauplius VI, insert without subdivision in the carapace;* ***b.*** *Euterpina, nauplius VI, muscles which cross, subdividing at insertion point in the carapace;* ***c.*** *Pseudodiaptomus, nauplius VI, with muscles which cross each other and subdivide, fan-like before insertion in the carapace.*

copepods, now classified in the order Poecilostomatoida (Bowman and Abele, 1982).

The naupliar mandible is a locomotive organ. In the Miracia nauplius it is a grasping organ (Fig. 5g), it fixes the specimen on to the substratum (a filament). The endopod and the exopod are fused and two strong spines and a seta permit the nauplius to hang on to the filament on which it lives.

During metamorphosis the mandible changes very little in the Calanoida - the mandibular blade widens or lengthens and forms the gnathobase with its indented border (Fig. 5b). It is probable that the crown of siliceous coating of the teeth is formed after metamorphosis, and this should merit an investigation. In the Augaptilidae the mandibular palp sometimes is very reduced (Fig. 5f). In the Arietellidae the endopod is reduced altogether.

In the Calanidae and nearest of kin, the vibration of the mandible plays an important role in the grazing movement. In the Oncaeidae and Corycaeidae the mandible is extremely reduced in the copepodids, which are carnivorous. The same happens with some mandibles of the Harpacticoida. The exopod usually suffers a stronger reduction than the endopod. In some copepodid mandibles the exopod and endopod are reduced to setae, but, in the Tisbidae and Porcellidiidae the contrary is the case: the mandible is well developed, especially the palp (see Lang, 1948). In the Canuellidae and Longipediidae the palp undergoes almost no change from the nauplius to the copepodid.

The first three pairs of appendages - general remarks and considerations

They are functional in the nauplius. While observing the nauplii, one is surprised at the variety of movements exhibited by the different forms (Fig. 7). The simplest locomotion is observed in Cyclopoida, Oncaea, and Corycaeus nauplii. Their three pairs of appendages move backwards and forwards, oar-like and the resulting movement is a jerk or impulse forwards or sideways in a more or less erratic fashion. The next simplest movements are those of some calanoid nauplii, such as in Acartia, which go round and round (Fig. 7b) in a continuous horizontal spiral or circle. Then there are the somersaulting movements or the movement in a vertical spiral of the calanid-paracalanid-clausocalanid hook-like nauplii (Fig. 7c). The Eucalanus pileatus nauplius has the most refined locomotion (Fig. 2a): it glides through the water very much like the adult calanoid when grazing. The Harpacticoida, apart from Longipedia and Sunaristes, exhibit very complicated naupliar movements (e.g. helicoidal) (Fig. 7d), or hardly any movements at all (as in Miracia when hanging on to a filament).

To explain these different types of locomotion the muscle system of the appendages has been investigated more closely by Fanta (1972a, b) and the results are compared in Figs. 6a, b, c, taken from Fanta (op.cit.). The simple movements of the Cyclopoida and other similar nauplii are thus explained by their simple almost parallel muscles which insert without subdivision in the naupliar carapace. The calanoid nauplii have a far more powerful muscle system, with intercrossing muscles, which insert in a fan-shaped (subdivided) manner in the carapace from the first naupliar stage onwards. The muscles of the harpacticoid nauplius, originally inserting without subdivision in the carapace (naupliar stages I to V), subdivide at the insertion point in the sixth stage, permitting a much more complicated locomotion than the one observed in cyclopoids, in Oncaea and Corycaeus.

From all the facts mentioned so far, we can arrive at some conclusions. It is generally accepted that the crustacean appendages were primitively more jointed. It is also a general belief that evolution

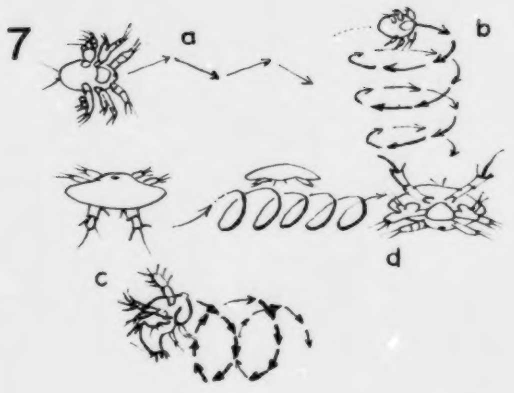


Figure 7. *Naupliar movements:* **a.** *Zig-zag motion of Oithona;* **b.** *Locomotion in circles of Acartia;* **c.** *Somersaulting Paracalanus;* **d.** *Helicoidal locomotion of an harpacticoid nauplius (taken from Bresciani, 1960).*

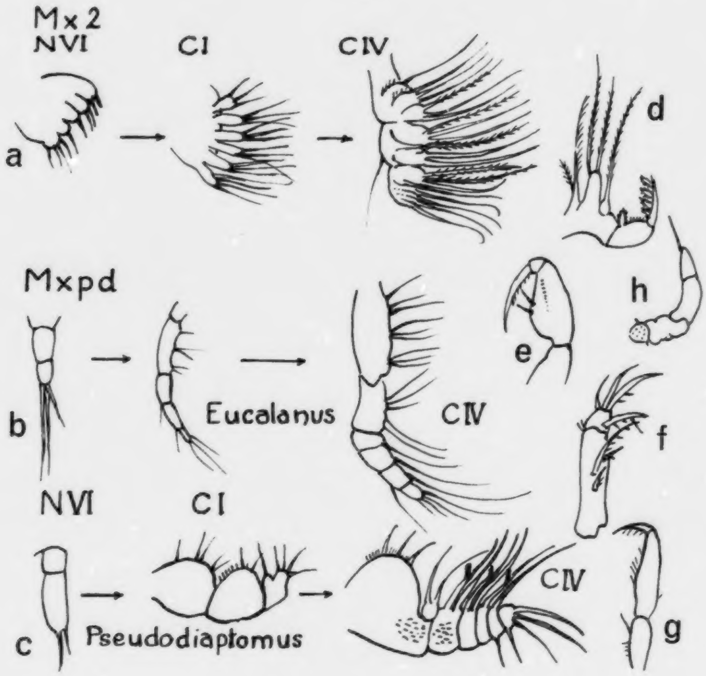


Figure 9. *Maxillae and Maxillipeds:* **a.** *naupliar maxillae (nauplius VI of Eucalanus pileatus), and copepodid maxillae of stage I and IV;* **b.** *maxillipeds of Eucalanus nauplius VI, copepodid I and IV;* **c.** *maxilliped of nauplius VI, copepodid I and IV of Pseudodiaptomus, in which the comb-bearing setae appear;* **d.** *the maxilliped of Acartia adult;* **e.** *the maxilliped of Oncaea adult;* **f.** *the same of Halicyclops adult (taken from Rocha, 1983);* **g.** *the same of Macrosetella adult;* **h.** *naupliar maxilliped of Chiridius (taken from Matthews, 1964).*

proceeds from simple and non-specialized forms to complicated and specialized ones in free-living organisms. If we compare the musculature of the nauplii, we find the simplest muscle system in the cyclopoids (Fig. 6e). The harpacticoid and the calanoid muscle systems are more complicated (Fig. 6d) and so is the locomotion of the nauplii. The primitive situation of appendages with several joints is also found in cyclopoids: the five-jointed antennule (Lescher-Moutoué, 1966), and the two-jointed endopod of the naupliar mandible. Interestingly the latter is present also in the most primitive harpacticoid nauplii (Longipedia and Sunaristes).

The only known nauplius which has an exopod of 10 joints on the second antenna (Fig. 4c) is a calanoid nauplius, judging from its general aspect and size. But, the other characteristics of the calanoid nauplii are not primitive.

If we compare the ornamentation of the appendages in the nauplii, we find the most elaborate type of spines and setae (Figs. 2d, e; 4d, e) in the Harpacticoida, the simplest again in the Cyclopoida. Thus, from the functional appendages of the nauplii we may conclude that of the three orders considered here, the most primitive copepods are the Cyclopoida, and, that the Harpacticoida and the Calanoida are derived.

The Harpacticoida Polyarthra (Longipediidae and Canuellidae) are either extremely primitive, or, they should constitute an intermediate order between the Cyclopoida and the Harpacticoida.

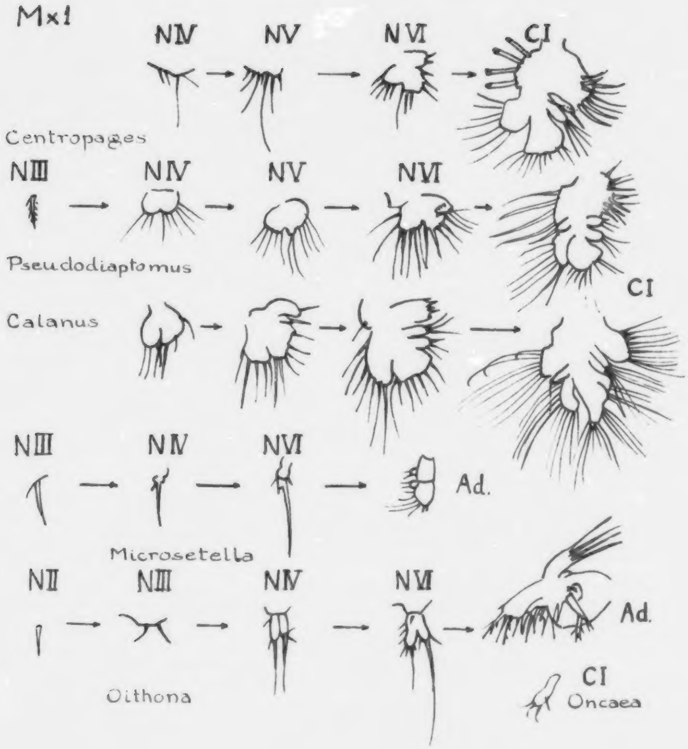
THE REMAINING APPENDAGES WHICH APPEAR AS RUDIMENTS IN THE NAUPLIAR STAGES (THE MAXILLULES, THE MAXILLAE, THE MAXILLIPEDS, THE FIRST AND THE SECOND PAIRS OF SWIMMING LEGS)

The maxillule

It is represented by a seta or spinule sometimes already in the third naupliar stage, or in the fourth stage by a heart-shaped, leaf-like structure (Calanoida) (Fig. 8, Pseudodiaptomus and Calanus). To the initial seta or spinule, more smaller spinules or setules are added in the next stage and the outline or the primordium of the future appendage. In the Oncaea nauplius V a rod-like structure with a long and a short seta develops from the rudiment present in nauplius IV. In the calanoid genus Acartia there are specific variations: the leaf-like rudiment only appears in the sixth nauplius in A. danae and A. lilljeborgi; in A. negligens it is not evident in nauplius IV. In the Harpacticoida the maxillule can also appear in the form of a simple seta, then a seta on an outlined lobe, and finally in nauplius VI, a lobe with a seta and several setules (Fig. 8, Microsetella). Longipedia and Oithona in the same stage have a maxillula rudiment similar to the heart-shaped structure of the Calanoida (Fig 8, Oithona).

The leaf-like structure protrudes from a ridge on the ventral shield of the naupliar carapace. The presence of this prae-coxa is not as evident in all naupliar stages as it is in Eucalanus pileatus, Metridia sp. and Pontellopsis sp. (Björnberg, 1972) where it takes the form of a basal plate.

The retarded development of the maxillule in some Harpacticoida (Phyllognathopus, Euterpina) is reflected in the development of the muscles which should move this appendage. Thus, in the sixth naupliar stage of Euterpina no muscles for the maxillule are present (Fig. 6b). In Oithona and Pseudodiaptomus small muscles are already visible in the nauplius VI to move the maxillary leaf-like structure (Fanta, 1972a). In the harpacticoid Tisbe the maxillules are relatively well developed in the


Mx1
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CI
Centropages
NIII
NIV
NV
NVI
Pseudodiaptomus
CI
Calanus
NIII
NIV
NVI
Ad.
Microsetella
NII
NIII
NIV
NVI
Ad.
Oithona
CI
Oncaea

Figure 8. *Maxillule - the Centropages maxillule of nauplius IV (NIV), nauplius V(NV), nauplius VI (NVI) and of copepodid I (CI); the Pseudodiaptomus maxillule of nauplius III (NIII), IV, V, VI and of copepodid I (CI); the Calanus maxillule of nauplius IV, V, VI and of copepodid I; the Microsetella maxillule of nauplius III, IV, VI and of the adult; the Oithona maxillule of nauplius II, III, IV, VI and of the adult (abbreviations as in the remaining figure); the maxillule of the first copepodid (CI) of Oncaea.*

nauplius V with two setae on each of the two podomeres which form the rudiment of the appendage (Johnson & Olson, 1948).

During metamorphosis the maxillule usually changes into its definite shape, but, with a smaller number of setae and spines than in the sixth copepodid. The internal lobes, as well as the exopod and the endopod of the maxillule are sometimes already outlined in the last nauplius stage of the calanoids (as in the Calanidae) (Fig. 8, *Calanus*). The maxillule can be very reduced in the first calanoid copepodid (*Pontellopsis*, *Acartia*, *Euaugaptilus*) and in some harpacticoid copepodids (*Macrosetella*, *Nitocrella*) in which, according to Lang (1948), two setae represent the endopod and the exopod. A greater involution of the maxillule is observed in *Oncaea* (Fig. 8, *Oncaea*).

It is usually believed (Gauld, 1966) that the function of the maxillule is to help in the feeding process. In the suspension feeders it composes the feeding chamber through which feeding currents pass leaving particles. These are swept off the setae by maxillary spines which also push the food particles into the mouth cavity. From Strickler's, Koehl's, Paffenhöfer's and Alcaraz' study of suspension feeding in copepods with microcinematography (the animal studied was *Eucalanus pileatus*) it was concluded that there is no filtering of water with retention of particles, nor circular currents by the beating of the mouth appendages. The second maxillae "actively capture parcels of water containing food particles" (Koehl and Strickler, 1981). "The endites of the first maxillae have an important role in pushing into the mouth the food particles obtained mostly by movement of the second maxillae". Unfortunately the authors last mentioned have not yet studied suspension feeding in copepods such as *Calanus finmarchicus*, *Centropages*, *Temora* and *Diaptomus*. In large containers I have observed circular feeding currents generated by *Pseudodiaptomus* (Fig. 3d, f). It would be interesting to know what microcinematography could reveal when applied to genera which have already been studied with other methods. From my own experience I find that each species has its own way of feeding.

The maxilla

It is also present in the fifth naupliar stage of some Calanoida, and, in the sixth naupliar stage of the Harpacticoida as a seta (or two setae) inserted on a ridge of the ventral shield, below the rudiment of the maxillule. In the next stage of the Calanoida it is composed of a crenulated ridge sometimes provided with minute spines or setules. During metamorphosis it acquires its definite shape and becomes functional, aiding in the feeding process. In *Candacia*, a carnivorous copepod, its setae are transformed into five strong spines (Gauld, 1966). Von Vaupel Klein (1984) summarizes the discussions about the interpretation of the composition of this mouth appendage.

Koehl and Strickler (1981) ascribe to it an important role in the catching of algae during the feeding process of *Eucalanus*. The outward fling of the maxillae creates a gap between them filled by the inrushing water and by the alga. Then they rapidly close in over the alga and water, which is squeezed out between the setae of these appendages and is pushed posteriorly by the first maxillae.

The maxilla in the carnivore *Candacia* is of greater importance than the maxilliped to hold the prey (Wickstead, 1959). In *Centraugaptilus* (Krishnaswamy et al., 1967) the maxilla has two rows of small buttons, non sensory, cuticular structures, which probably function as adhesive plates to hold the prey. In *Oncaea* the maxilla is reduced to a pincer-like structure which must be very efficient in grasping and holding the victim, even in piercing it for later sucking. Wickstead (1962) described a similar behaviour for Corycaeidae. In *Oithona* the maxilla of the copepodids is provided with long stout, spiny spines or thick spiny setae which together with the maxillipeds, similarly structured, grasp the food from the surrounding medium (Gauld, 1966). In Macrosetella the maxilla is very much reduced and also ends in the form of a pincer, thus being an effective grasping organ with which the animal holds the Trichodesmium filaments on which it lives. Vermiform and brush-like setae of the maxillae of several families of Calanoida and Harpacticoida are probably sensory and attachment organs.

The maxillipeds

They usually are present in the sixth naupliar stage in the form of a pair of long tongue-like bands, disposed laterally to the midventral line, and, situated between the maxillules (Fig. 9b). At their tip they carry 2 or more setae. During metamorphosis the maxilliped acquires its almost definite shape. It is uniramous from the naupliar stages. In the Pseudodiaptomus first copepodid it has three podomeres (Fig. 9c); in the second, five; and, in the third, it already displays the seven podomeres of the adult. The specialized setae of the endopod, which carry little comb-like structures for scraping the substratum or for cleaning the other appendages, are present from the fourth copepodid stage to the sixth of Pseudodiaptomus (Fig. 9c).

The maxilliped is formed by the praecoxa, the coxa or coxopod, the basipod and the endopod. In Macrosetella (Harpacticoida) the endopod is represented by a hook (Fig. 9g). In Sunaristes and Cerviniopsis, considered primitive Harpacticoida, the four podomeres are also present (Lang, 1948). In their nauplius there is no indication of a praecoxa or of any other podomeres in general. Some nauplii, those of Eucalanus attenuatus, show a suture across the tongue-like flap which is the rudiment of the maxilliped in nauplius VI (Fig. 9b). In Chiridius armatus, Matthews (1964) found a well developed minute appendage with four podomeres and a terminal seta in the last naupliar stage (nauplius IV in this species)(Fig. 9h). The maxilliped may be very reduced relative to the maxilla, in both the nauplius and the copepodid (Acartia, Pontellidae)(Fig. 9d). Euchaeta has the longest naupliar maxilliped known (Sazhina, 1982) and one of the most developed copepodid maxillipeds.

The function of the maxilliped, when reduced in size, is to shut the feeding basket in calanoids such as Acartia, and in cleaning the other appendages. In Euchaeta, a carnivore, the combined action, first of the maxillipeds, grasping the prey, then of the maxillary setae closing up below its body, holding it against the underside of the head, permit the tearing off of pieces of the prey by the maxillulary endites and the toothed edges of the mandibles (Wickstead, 1962; Gauld, 1966).

In the Cyclopoida of the genus Halicyclops Norman (Fig. 9f), and in Graeteriella Brehm, as well as in commensal genera, which do not need this appendage for feeding, the maxilliped is very reduced. It is very developed in the genus Oithona where it is used for catching food, and in the Poecilostomatoida, chiefly in the males, where it is prehensile for holding the female during copulation (Fig. 9e).

The swimming legs

The first pairs of legs usually are present in the last naupliar stage as a pair of foliaceous structures situated posteriorly to the outline of the maxillipeds and carrying spines and/or setae on their posterior border. In Cyclopoida and Harpacticoida there sometimes is a pair of simple foliaceous structures or just a pair of ridges from which setules or spinules protrude. In the last nauplius stage of Chiridius armatus the first swimming leg is distinctly composed of four podomeres, two basal ones, an endopod and an exopod. The spines and setules mayx or may not be present in the nauplius. In none of the observed primordia of legs was it possible to find any indication of a praecoxa.

During metamorphosis the foliaceous structures of the nauplius change into the legs proper, which usually have a coxa or coxopod, a basipod and endo- and exopod, generally undivided, or composed of two podomeres as in the exopod of the second leg. The first copepodid already shows the rudiments of the third pair of legs; the second copepodid, of the fourth pair of legs; the third copepodid, of the fifth pair of legs. The fourth copepodid and the fifth copepodid (sometimes as early as the third copepodid) show differences in the fifth pair of legs which permit the distinction between males and females in the Calanoida. The Harpacticoida, judging from Euterpina acutifrons, show a differentiation of the male and female appendages only the moult of the fifth copepodid (Haq, 1965). The sixth pair of legs appears in the fifth copepodid stage of the Harpacticoida, but, disappears in adult females. In the Oithonidae the copepodid V shows sexual dimorphism; the male already has a fifth and a sixth pair of legs represented by setae; the female has the fifth pair only, according to Uchima (1979).

Specific differentiation of the swimming legs is easily observed in the first pair of the Harpacticoida and in the fifth pair of the Calanoida, from a taxonomist's point of view. The sixth pair of legs also presents specific features in the Cyclopoida. The fifth pair suffers changes in the females of the Calanoida, Harpacticoida and Cyclopoida to facilitate the attachment of eggs or of egg sacs in those species which do not lay their eggs directly into the sea water, or on the bottom of the sea. In the males of the Calanoida the fifth pair of legs is considerably changed in some species, undergoing a differentiation on the left and on the right side in order to grasp the female with one leg while the other places the spermatophore on the genital segment of the partner. Among the Calanoida and the Harpacticoida there are species which retain their fifth legs or their first legs respectively, hardly unchanged (some Calanidae, Megacalanidae, Canuellidae, Longipediidae and Cerviniidae). These are undoubtedly more primitive than those which show numerous adaptations.

In those copepods which lay their eggs freely there is a great reduction, even to complete absence of the fifth pair in order to facilitate the swimming movements (see Von Vaupel Klein, 1984).

The remaining legs from the second to the fourth pair usually are composed of a coxa or coxopod, a basipod, an endopod with three podomeres and an exopod of also three joints. In the Calanoida there may be a reduction in the number of podomeres of the endopod of the first and second legs (Aetideidae, Phaennidae) and in others the exopod may also suffer a reduction of podomeres (Euchaetidae). In Paroithona the endopods of all legs are reduced to two podomeres.

As for the ornamentation of the legs there are also great variations, but, usually the coxopods and the basipods bear one or two setae, the endopods have plumose setae, one on the first, two on the second and generally five or more on the last podomere. There may be reduction of these setae or they may be substituted by spines, partially or totally. The exopod in most species is ornamented with spines (five or six) externally, a terminal spine of various shapes and there are plumose setae (six or more) internally. There can also be a reduction in the number of these setae. Pores of glandular cells (such as mucus glands, luminous glands, and others), patches of fine hair-like setules, tufts of bristle-like spines, perforations, scale-like structures, etc. may also be present on the face of the several podomeres which compose the swimming legs (Clarke et al., 1962; Campaner, 1978; Verdinelli, 1981; Von Vaupel Klein, 1984). Generally, the most complicated and varied ornaments of the appendages are found in the benthic or plankto-benthic Calanoida and Harpacticoida (excepting the Longipediidae and the Canuellidae).

CONCLUSIONS

From the study of the naupliar appendages, one has to agree that, by the accepted standards of primitiveness, the cyclopoid nauplius presents the greatest number of primitive features. It is also a fact those the Poecilostomatoida the nauplii of which are known, have cyclopoid nauplii. The next most primitive nauplii, judging from the appendages, are the Longipedia and the Canuellidae nauplii, among the Harpacticoida. All the other nauplii of the Harpacticoida are far more advanced in their most developed stage (the fifth) than any of the known Calanoida or Cyclopoida nauplii.

To decide whether a group of animals is older or younger than others the adaptive radiation can also be used. A group which is found in the greatest number of environments, with the greatest number of most diverse species occupying the most varied niches has the probability of being older, or of having inhabited the world for a longer period of time than the other groups.

If we look at copepods we find the Harpacticoida with a greater number of species in the marine benthos, with one or two terrestrial species, and with several in freshwater. The Calanoids have most species concentrated in the marine plankton, some in the planktobenthic community, a few almost benthonic, and few species in freshwater. The Cyclopoida are well established in the marine environment and in freshwater where they have invaded the benthos, the plankto-benthos and the plankton, and there are many commensals, parasites and species associated with other animals (which have now been separated into different orders). From the naupliar evidence and the adaptive radiation it seems that of the three groups considered in this paper the Cyclopoida is the oldest group of copepods established in the world.

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2. Growth, Life History and Culture (Chairman: *C.R. Corkett*)

SYMPOSIUM ON GROWTH, LIFE HISTORY, AND CULTURE

Introduction by Dr. C.J. CORKETT

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Welcome to the symposium on Growth, Life History, and Culture. We have mixed bag of topics for this afternoon's session. Although two speakers will be dealing with their field investigations all the distinguished speakers in this session have extensive experience in the laboratory investigations of live copepods.

For this reason, I should like in this short introduction to share with you some thoughts on copepod rearing and cultivation. Copepod cultivation has developed along two basic lines. The first of these we may call "the laboratory rat line" in which laboratory populations are cultivated and used in variuos investigations such as genetic, toxicological and biochemical studies.

The harpacticoids were initially first favoured in laboratory culture because of their relative ease of maintenance. Genera such as Tisbe - used in the laboratory of Battaglia - and Tigriopus - used in the laboratory of Provasoli - have been good workhorses.

No doubt my analogy of copepod populations with laboratory rats has many simplifications but one of the more important is that continuous cultures of calanoid copepods have never been established in the way that different strains of rats maintained. All laboratory populations of the calanoids need occasional replenishment from wild populations. We do not now consider this too surprising but 20 years ago in the early sixties I think we were more optimistic. At that time my old friend Ed Zillioux working at the Naval Research Laboratory in its facilities at Cheasapeake Bay had established cultures of Acartia tonsa in the defined media of a completely artificial sea water.

Recently a record 60 generations for Centropages hamatus has been established by our first speaker and we are therefore now well on the way to maintaining truly continuous cultures of calanoids.

The second way in which copepod cultivation has developed we may call "fish food line" and although we do not have speakers in this session concerned with aquaculture, there are several delegates at this Conference who have this interest and we have heard from Dr. Kahan and Dr. James this morning.

Despite their importance in nature, copepods have never been the first choice for live foods in hatcheries - whether you are talking about flat fish hatcheries in the U.K. or penaeid shrimp hatcheries in Japan, the first choice live foods have been the rotifer Brachionus and the brine shrimp Artemia.

The question is what are the chances that copepods may supplement or take over these roles? There seems to be two immediate ways in which copepods may achieve important status as fish foods.

Firstly, with their continued use the price of Artemia eggs may rise enough to make copepods a viable alternative.

Secondly, there is a medium size category - i.e. after the use of Artemia as food - that could be filled by copepods.

In the short term, rotifers will be difficult to replace as a first live fish food because of their optimum size; Artemia will probably remain standard while it is available and artificial and prepared feeds will continue to prevail because of their low costs.

In the long term, however, the role of copepods as live fish food will become more important. Artemia and Brachionus will gradually be replaced by different sized naupliar and copepodite stages since these stages are much more effective in initiating a feeding response in larval fish.

CULTURE AND DEVELOPMENT OF *TEMORA LONGICORNIS* (COPEPODA, CALANOIDA) AT DIFFERENT CONDITIONS OF TEMPERATURE AND FOOD

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Abstract: Pelagic marine copepods were cultured in the laboratory and bred through multiple generations at 15°C and a constant supply of autotrophic algae as food. The heterotrophic dinoflagellate *Oxyrrhis marina* introduced in the copepod cultures was important in controlling the water quality by consuming much of the autotrophic algae. At the same time *Oxyrrhis* was an important additional food item for the copepods.

Using the offspring from this culture system 4 replicate generations of *T. longicornis* were raised from N I and II to adult copepods at 16 different combinations of temperature and food concentration. Food was regulated by the supply of algae, which led to proportional changes of the *Oxyrrhis* concentration. The rate of development increased with each increase of food supply and temperature.

In contrast to earlier observations development was not isochronal, even at optimal food levels. It appears to be very difficult to meet all the requirements for isochronal development. It is proposed that the quality of the food is important, in particular since the size of adequate food organisms may change continuously during development.

The relation between development time and temperature was described by Bělehrádek's functions. At different food levels the curves differed in their constant of proportionality (a), the other parameters (α and b) seemed to be independent of food level.

INTRODUCTION

It is not easy to estimate the growth of copepods in natural populations. Due to continuous reproduction and fast development copepod populations tend to consist of all developmental stages simultaneously, which makes it difficult to track the different cohorts during the season. Another main problem is that very little is known about the specific growth conditions during the various life stages of copepods. Without a thorough knowledge of the type of food consumed and its amount required at different temperatures, quantifying the overall phytoplankton biomass to characterize zooplankton food condition may be similar to counting sand grains together with the seed in a chicken coop as a measure of food supply. The influence of food concentration and temperature on development of copepods can be studied most conveniently by raising cohorts of single copepod species under well defined conditions of temperature and food in the laboratory.

In the last 2 decades much progress has been made in the cultivation of pelagic copepods. Starting with simple but laborious methods to breed copepods through one or more generations (i.e. Zillioux and Wilson, 1966; Corkett, 1967; Mullin and Brooks, 1967; Katona and Moodie, 1969), gradually more complicated techniques were developed to improve the culture conditions (i.e. Zillioux, 1969 and Paffenhofer, 1970). A complete picture of this development can be obtained by consulting Omori (1973), Kinne (1977), Paffenhofer and Harris (1979), and Davis (1983). A major problem in copepod cultivation seemed to be the control of the water quality. Recently it was shown that no complicated techniques are required for continuous cultivation of various copepod species, if the water quality is controlled by the heterotrophic dinoflagellate *Oxyrrhis marina* (Klein Breteler, 1980; Klein Breteler and Gonzalez, 1982).

By culturing copepods several authors have studied the effect of temperature (Mullin and Brooks, 1970a; Landry, 1975; Uye, 1980; McLaren and Corkett, 1981; Thompson, 1982; and Uye et al., 1983) or food concentration (Mullin and Brooks, 1970b; Paffenhofer, 1976; Harris and Paffenhofer, 1976a,b; Klein Breteler et al., 1982; Davis, 1983) on development and the growth rate of pelagic copepods. The effect of both temperature and food concentration has only been studied for Calanus helgolandicus (Mullin and Brooks, 1970b), the copepodite stages of C. pacificus and Pseudocalanus sp. (Vidal, 1980a,b) and the freshwater species Boeckella symmetrica (Woodward and White, 1983). The present paper concentrates on the rate of development of Temora longicornis cultured under 16 different combinations of temperature and food. Some attention is paid to the mortality rate to illustrate the effect of the various conditions on the copepod population.

MATERIAL AND METHODS

The calanoid copepod Temora longicornis (Müller) was isolated from the Dutch Wadden Sea and cultured continuously in the laboratory under standard conditions of 15°C and optimal food, as described by Klein Breteler (1980) and Klein Breteler et al. (1982). Brood from this parental stock was raised to maturity in 4 independent experiments, each at 4 different temperatures and 4 food levels. Animals used represented the 9th to 14th generation bred in the laboratory.

At the start of each experiment larvae were separated from the parental culture by sieving part of the water through a nylon screen with a mesh-size of 106 μm, allowing N I and II with a few concomitant eggs to pass. They were concentrated in the old culture water, mixed well, and divided equally into fiberglass containers of 25 l. Sea water of about 30 °/oo was added up to 22 l through a Whatman Gamma 12 tube filter (pore-size < 2 μm) to a final concentration of about 40 animals per l. The amount of old culture water accompanying the larvae to the tanks was kept low (less than 0.2 l) in the last 3 experiments, but in the first one this source of contamination was not considered, and considerably more (1-5 l) food-rich old culture water was also introduced in the containers. In 2 of the 4 experiments the number of larvae was insufficient to supply all 16 tanks simultaneously. These experiments were set up at 1 or 2 temperatures at a time and brood collected from the same parents during the next days was used to complete them at other temperatures.

At regular time intervals the concentration and the stage of development (Klein Breteler, 1982) of the copepods was determined. After stirring, samples were taken with a pvc-tube (diameter 4 cm) reaching almost to the bottom of the tank. A stopper with a hole on the top and a dismountable sieve (50 μm) on the bottom of the tube allowed easy sampling and collecting of the animals in a small petridish. Usually 4 samples of 0.25 l were taken, but additional samples were taken if less than 10 animals were caught. Depending on culture conditions sampling was performed 1 to 3 times per week, to obtain 8 or more samples during 1 generation. The temperature was maintained within the natural range at 5, 10, 15 and 20°C (± 0.2°C) by keeping the copepod containers in racks immersed in temperature-controlled water basins. The experiments were carried out from May till December 1983 at strongly dimmed natural light conditions.

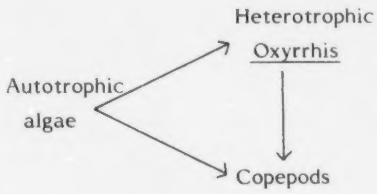
Food for the copepods was obtained from 2 chemostat cultures of Rhodomonas sp. and 1 of Isochrysis galbana, kept at 15°C on f/2 medium (Guillard, 1975) at a dilution rate of 0.17 d^{-1}. The mean spherical diameter of Rhodomonas was 6.7 μm, of Isochrysis 4.9 μm; the concentrations were 2.0 and 5.4 $.10^6$ cells per ml, respectively. Two times per day time-regulated peristaltic pumps fed 9.3, 2.3, 0.6 and 0 ml from each of these cultures to the copepod cultures, representing the food levels 1, 1/4, 1/16 and 0. The volumes fed were chosen lower than before (Klein Breteler et al., 1982) since both the size and the concentration of the algae had increased significantly in the course of years.

Although normally the heterotrophic dinoflagellate Oxyrrhis marina was not fed, it did occur in all copepod cultures as it was introduced, together with the copepod larvae, with some of the old culture water at the start of the experiments. Only when Oxyrrhis was grazed down by the older stages of copepods towards the end of an experiment, it was added to maintain the original concentration. To this end Oxyrrhis was cultured separately as a stock in a 2 l continuous culture at a dilution rate of 0.23 per day. This culture, kept in the dark, was fed continuously with the yield from a 3rd Rhodomonas continuous culture, and contained about 1.10^5 Oxyrrhis cells per ml, with a mean spherical diameter of 13,2 µm.

Concentrations of algae and Oxyrrhis were measured weekly using an Elzone particle counter (Particle Data Inc.). More frequently concentrations were examined superficially by microscope to adjust the Oxyrrhis concentration when necessary. Cell concentrations were converted to carbon concentrations according to Klein Breteler et al. (1982), after a volume correction for the increased size of Isochrysis and Rhodomonas. Thus Isochrysis contained 11.7, Rhodomonas 33.1 and Oxyrrhis 215.8 pgC per cell. All particles counted within the size spectrum of these flagellates were considered to be these organisms, also at food level 0 when no Isochrysis and Rhodomonas were fed at all.

RESULTS

Culture system. - If the colourless Oxyrrhis marina is introduced in a copepod culture it consumes most of the (excess of) algae fed to the copepods. Being an active swimmer this flagellate remains well in suspension, and thus prevents accumulation of organic matter on the bottom of the culture tank. Oxyrrhis appears to be readily eaten by very young stages of copepods (unpublished grazing experiments). Together with the autotrophic algae these food organisms almost cover a size range of 3.6-20 µm spherical diameter (Fig. 1). Since this corresponds to a cell length of Oxyrrhis up to 35 µm a wide food spectrum exists in the culture, which may be important to fulfill the requirements of the copepods at the various stages of development.



The short two way food-chain shown in the diagram leads to a roughly stabilized concentration of food organisms in the copepod cultures. The average food concentrations are shown in Fig. 2. At all food levels the biomass of Rhodomonas was very low. In spite of its smaller cell size, the carbon concentration of Isochrysis was an order of magnitude higher. Preying upon these autotrophs, Oxyrrhis still reached a much higher biomass at all food levels. On average 73 % of total food biomass was contributed by Oxyrrhis, 24 % by Isochrysis, and only 4 % by Rhodomonas. Obviously Rhodomonas is the

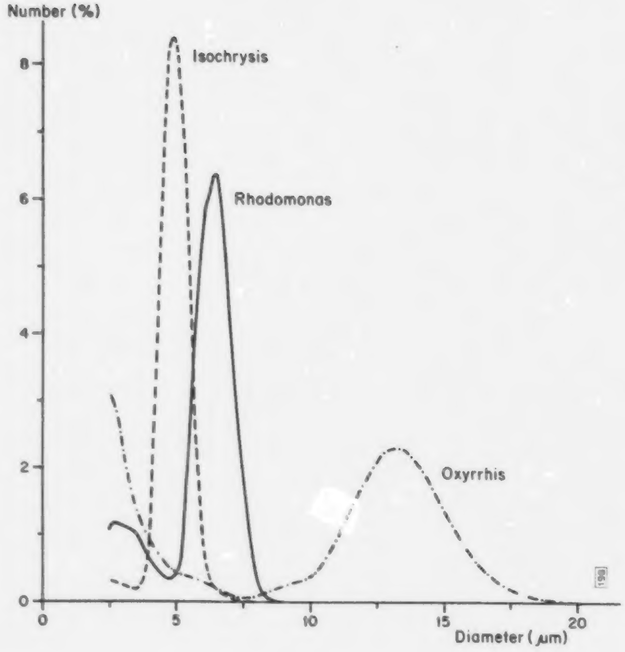


Figure 1. *Relative number at different spherical diameter (um) of the algae Isochrysis galbana and Rhodomonas sp. and the heterotrophic Oxyrrhis marina. Curves obtained from individual continuous cultures of each species.*

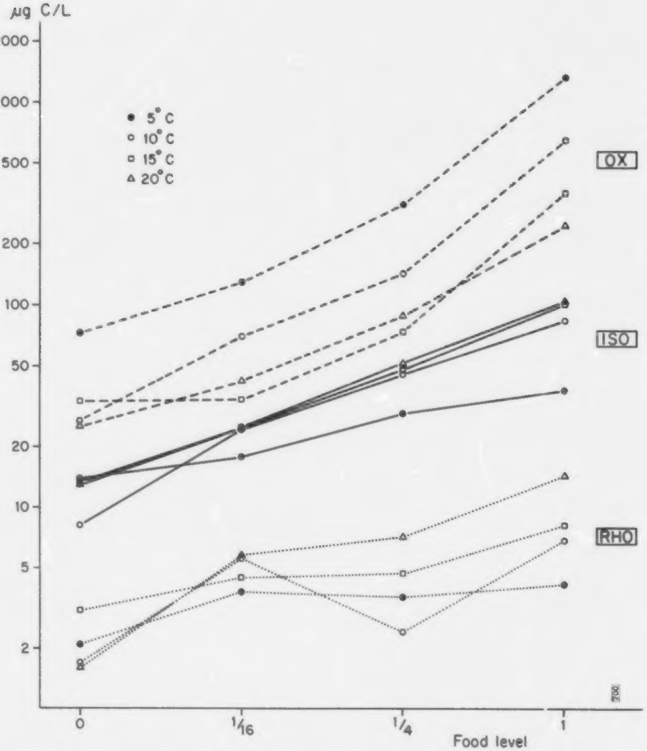


Figure 2. *Concentrations (ug/l) of the autotrophic algae Rhodomonas sp. (dotted lines), Isochrysis galbana (solid lines) and the heterotrophic Oxyrrhis marina (broken lines) in the cultures at different food levels and temperatures.*

favourite food of Oxyrrhis.

The concentration of Rhodomonas and Isochrysis increased with the amount fed (Fig. 2). At food level 0, when no autotrophic algae were fed, still significant concentrations of similar sized particles (detritus and other heterotrophic flagellates) were present together with Oxyrrhis. The concentration of Oxyrrhis also increased sharply at higher food levels, apparently being strongly controlled by the supply of autotrophic algae. Temperature had a significant influence on the concentration of these organisms, which was different for the autotrophs and Oxyrrhis. Whereas the concentration of Oxyrrhis generally decreased, that of the autotrophs increased at higher temperatures. Although this may be a direct effect of the increased temperature, it is also possible that a concomitant higher metabolism and consumption of the copepods contributed to the lower Oxyrrhis concentration. In turn, a lower concentration of Oxyrrhis doubtlessly led to a lower predation of this organism on Rhodomonas and Isochrysis, and hence indirectly to the adverse effect of temperature on the concentration of these algae and Oxyrrhis. As a result of the food levels chosen a total food biomass was obtained which increased 2 to 3 fold at each higher food level (Table I).

Table I. *Mean total biomass ($\mu g\ C.l^{-1}$) of algae and Oxyrrhis at different temperature and food levels in cultures of Temora longicornis.*

Food level	**Temperature °C**			
	5	10	15	20
0	90	37	51	41
1/16	153	100	64	73
1/4	349	196	128	149
1	1420	750	462	370

Copepods. - The development of Temora at 10°C and at 4 different food concentrations is demonstrated in Fig. 3. At this temperature the development observed in the 4 replicate experiments can be described by 2 straight lines, with an inflection point between N V and C I. This means that the duration of all stages was not constant, hence development was not isochronal. Generally the data from the 4 individual cultures corresponded well to the regressions calculated. Differences in stage level between cultures are partly introduced at the start of the experiments by differences in age of the larvae and, more importantly, by differences in organic load of the culture water. Especially in our first experiment (symbol 0 in Fig. 3) old, food-rich culture water accompanied the larvae at the start more than in the other experiments. Of course such initial injection with food is most sensitive at the lowest food level, as appears from the relatively fast development in this first culture during the initial 10 days at food level 0.

The regressions have been calculated and drawn in Fig. 3 up to the day when adult copepods were found in one of the replicate cultures. At this time the copepods had reached C V on average. Later data points deviate from the regression due to accumulation of animals in the adult stage. This implies

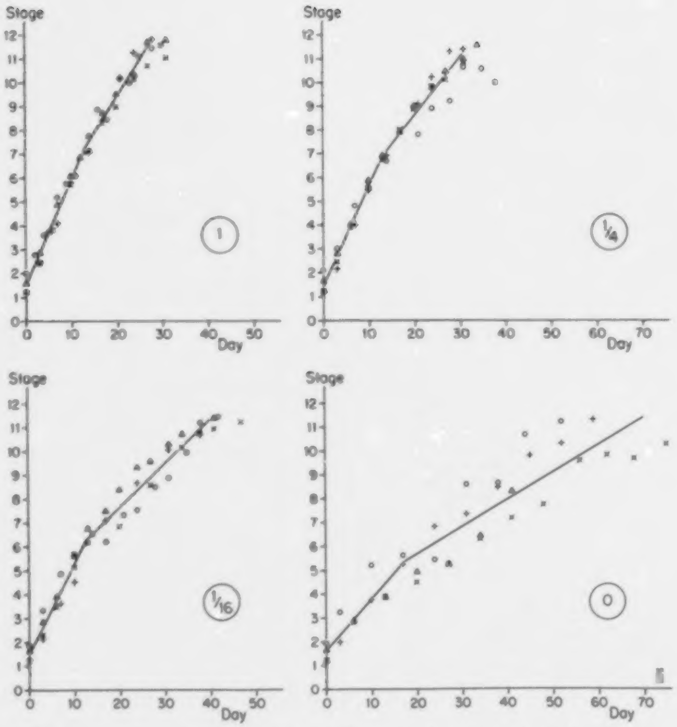


Figure 3 The development of Temora longicornis cultured at 10°C at food level 1, 1/4, 1/16, and 0. Mean stages indicated by eggs (0), and nauplii (1-6), and copepodites (7-12) in 4 replicate cultures (different symbols). Regression lines calculated at arbitrary time intervals.

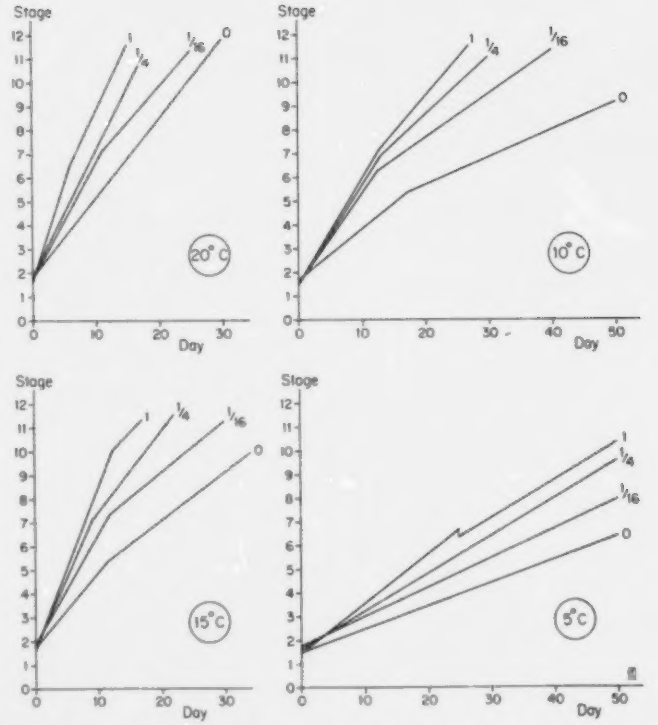


Figure 4. The development of Temora longicornis cultured at 20, 15, 10 and 5°C and food level 0, 1/16, 1/4 and 1. Regression lines calculated as in Fig. 3, but drawn not beyond the 50th day.

that here the regression method does not allow a proper estimation of the development rate between C V and C VI.

The data shown for 10°C are quite representative of the results obtained at other temperatures. The only exception is that at 5°C at food level 0 and 1/16, and at 15°C at food level 0 adult animals were present already when the population consisted mainly of C IV. The regression lines (Fig. 4) demonstrate that the development proceeded faster at increasing temperature and food level. The difference between 15 and 20°C was relatively small. Experiments at the extremely high food level 4 at 5 and 10°C (unpublished observations) and 15°C (Klein Breteler et al., 1982) indicated that food level 1 is sufficient for optimal growth. At this optimal food condition development was not isochronal (Fig. 4), although at 15°C the development rate was constant through C III. Only sometimes under suboptimal conditions (20°C, food level 0, 1/4, and 5°C level 0, 1/16, and 1/4) growth of nauplii and copepodites was described by one regression. Mostly, however, the development changed to lower rates between N V and C I.

Using the reciprocal value of the slopes of the lines in Fig. 4 (Table II) the duration of each stage was calculated, and the total development time from N I to C VI plotted against temperature at different food levels (Fig. 5). Curves were fitted according to McLaren (1963, 1965), using Bělehrádek's function $D = a(T - \alpha)^b$, in which D is the duration (days) and T the temperature (°C). The parameters *a* and *b* (Table III) were obtained by varying α and selecting the regression with the highest correlation coefficient at each food level. Only at food level 0 the correlation coefficient continued to increase at decreasing α. Since differences in *b* appeared to be not significant (Table III), and since *b* is suggested to be constant within species (McLaren et al., 1969) the average *b* of the other 3 curves was adopted to calculate α from the regression at food level 0. The curves found describe the data quite well, except at food level 0. At this food level a simple curve clearly cannot fit to the points. Nevertheless at all food levels more or less parallel curves were obtained with an average value *b* of -0.62 and α of 2 to 3. Assuming this mean value of *b* for all food levels, the proportionality constant *a* clearly reflects the effect of food concentration (Table III). The parameters observed differ greatly from those calculated by McLaren (1978) for Temora longicornis from hatching to 50 % adult at excess food (Table III), which is reflected by the different shape and level of the curve at food level 1 (Fig. 5). (See also Discussion).

The rate of mortality (Z) was calculated over the whole of each culture period according to $Nt = No.e^{-Zt}$, in which No and Nt are the concentration of animals per l at time 0 and t, after correction for mortality due to the sampling, and t is the time of cultivation in days (Table IV). At 5 to 15°C beyond food level 0 mortality was relatively low, between 0.021 to 0.041 per day. At food level 0 and at 20°C also at higher food levels mortality was much higher. Moreover, at food level 0 in 3 single cultures mortality was so high that the copepods were exterminated before reaching stage N VI to C II. Usually when mortality rates were low they were constant at the same time. But at high mortality it often occurred that the mortality rate increased during cultivation. Generally this increase took place during N V to C I, sometimes extending to all older stages.

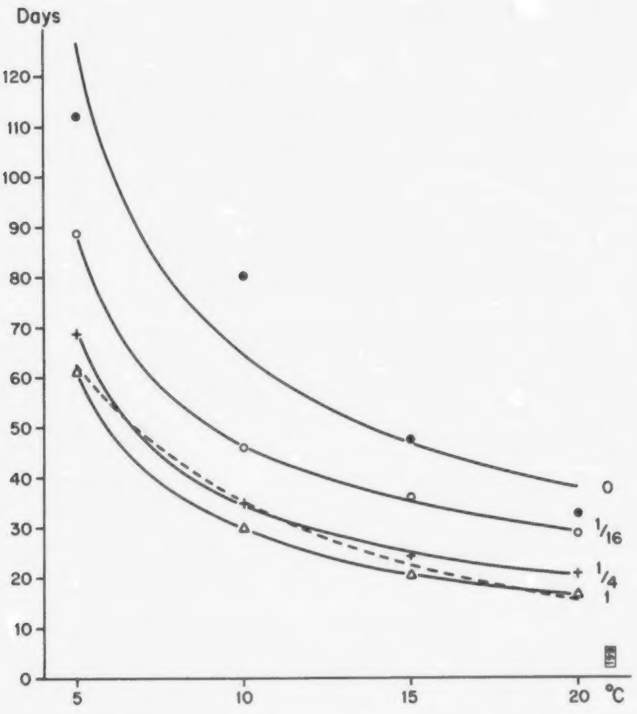


Figure 5. *Development time (days) of Temora longicornis from N I to adult plotted against temperature (°C) at food level 0, 1/16, 1/4 and 1. Belehrádek's functions fitted (solid lines) and compared with the curve given by McLaren (1978) for T. longicornis (broken line).*

Table II. *Rate of development* (d^{-1}) *(slope of the regression lines in Fig. 3) from the stage indicated to the next stage.*

Food level	**Stage**	**Temperature °C**			
		5	10	15	20
0	1- 4	0.098	0.213	0.316	0.335
	5-11	0.098	0.114	0.202	0.335
1/16	1- 5	0.124	0.375	0.464	0.490
	6	0.124	0.184	0.464	0.490
	7-11	0.124	0.184	0.216	0.303
1/4	1- 6	0.160	0.415	0.600	0.530
	7-11	0.160	0.245	0.345	0.530
1	1- 5	0.209	0.439	0.685	0.833
	6	0.161	0.439	0.685	0.565
	7- 9	0.161	0.306	0.685	0.565
	10-11	0.161	0.306	0.273	0.565

Table III. *Parameters of Bělehrádek's function* ($D = a\,(T-\alpha)^b$) *of generation time (D) and temperature (T) at different food concentrations. Values calculated with the mean b = -0.62 from food levels 1/16, 1/4 and 1 in parentheses. 95 % confidence limits of b indicated. Data at excess food from McLaren (1978).*

Food level	**α**	**b ± 95 % conf.**	**a**	**correlation coefficient**
0	(2.5)	(±0.60)	(222)	(-0.95)
1/16	2.9 (2.0)	-0.53 ±0.07	131(174)	-1.00
1/4	2.7 (2.6)	-0.60 ±0.06	114(118)	-0.99
1	2.1 (2.9)	-0.72 ±0.06	132 (98)	-0.99
excess	-10.4	-2.05	16988	

DISCUSSION

At a continuous supply of autotrophic algae our culture system led to more or less stable concentrations of the 3 different food organisms. The balance between the algae and Oxyrrhis appeared to be affected by temperature, perhaps by a temperature dependent consumption of Oxyrrhis by the copepods. Apart from this possible effect, the copepods seemed to exert little influence on the food organisms during most of the cultivation period. Only at suboptimal food levels when mortality had been low, many late copepodites were able to graze down the Oxyrrhis population. This resulted in an immediate increase of the concentration of algae and necessitated manual intervention.

Due to the effect of temperature food concentrations were not quite the same within the food levels chosen for the experiments. Since Oxyrrhis was the dominant food organism, the total food biomass was higher at lower temperatures. At food level I this has probably not influenced the growth rate of the copepods, since this food level was found to be excessive. However, at lower food levels the growth rate may be overestimated at lower compared to higher temperatures.

Although strictly isochronal development probably does not occur, (Landry, 1983) it was typically approached at optimal or slightly suboptimal food conditions of Temora and 3 other copepod species (Klein Breteler et al., 1982). Surprisingly, however, at the highest food level the present results did not show isochronal development. After re-inspection of the data of Klein Breteler et al. (1982) at food level I it seemed that in 14 out of 39 Temora cultures development was possibly lower after stage N VI to C III, which became masked because of the compilation of all cultures in one figure. The fact that in most cultures the development rate remained high after N VI suggests suboptimal conditions in the cultures with declining rates. In the present study lowered growth rates occurred mostly between N V and C I (Fig. 4). Increased mortality rates also occurred after N V at extreme culture conditions (20°C, or food level 0). This indicates that late naupliar and all copepodite stages are vulnerable to suboptimal culture conditions, possibly some kind of disease or bacterial contamination which apparently takes place at times even when food is plentiful. The quality of the algae may not always be constant either. The results show that it is not easy to reproduce exactly the optimal development through all stages, even when food is offered ad libitum as a mixture of food organisms. Therefore failure to detect isochronality does not necessarily mean that it does not exist, but may as well be attributed to inability to feed the older stages with the appropriate quality of food.

Only limited data are available on the influence of food quality on growth and development of copepods. The algal species offered as food greatly affected the growth rate of Calanus helgolandicus (Paffenhofer, 1970, 1976) and Rhincalanus nasutus (Mullin and Brooks, 1970a). In view of the phytoplankton biomass available in Loch Striven and the continuing growth of younger stages, McLaren (1978) concluded that natural food concentrations are not limiting the growth of Pseudocalanus minutus in stage C IV and Calanus finmarchicus in stage C V, while nevertheless the copepodites in these stages were in arrested development. However, a high phytoplankton biomass does not guarantee that the specific needs of the different copepod stages are met. This was strikingly demonstrated by observations of maximum development rates of Temora at a Thalassiosira rotula biomass of 50 µg C/l (Harris and Paffenhofer, 1976b), whereas Acartia tonsa could not be satiated in natural sea water containing as much as 2000 µg C/l (Durbin et al., 1983).

The requirements of particularly the larger copepodite stages are not easily met. When a single food organism was offered (Harris and Paffenhofer, 1976b) maximum growth rates of Temora copepodites were lower than in the food mixture of our culture system. In the North Sea in summer the growth rate of the older stages of copepods was shown to be suboptimal (Klein Breteler et al., 1982; Daro and van Gijsegem, 1984). Also the weight of C. helgolandicus was affected by food quality only during the last stages of development (Paffenhofer, 1976).

For Calanus pacificus and Pseudocalanus sp. Vidal (1980a,b) demonstrated that the food concentration necessary for optimal growth and development increases with the stage of copepodite development. This once more draws attention to the problem how to satisfy copepodites at old stages of development. However Vidal (1980a) neglects the effect of food quality, yet his Fig. 2 indicates very clearly that different species and clones of diatoms affect the growth rate of C. pacificus. At similar algal concentrations a distinctly higher growth rate can be observed at each increase of diatom size in 24 out of 30 experiments. Obviously the size of the diatoms used had great influence on the growth rate of C. pacificus copepodites. Since Vidal used single species of algae as food for different copepodite stages, his evidence for a dependency of optimal food concentration on developmental stage, may be based on a progressively changing demand of food quality during development to maturity.

Under natural conditions the development of copepods is determined by temperature and food condition. In spring low temperatures prevail together with generally high food concentrations, which may consist importantly of diatoms of perfect food value. Under such conditions the generation time of Temora can be expected to be about 40 days (Fig. 5). Later in the season the higher temperature would allow a much quicker development if the food situation had remained the same. However, less edible diatoms and flagellates may predominate in summer with important consequences in particular for the larger copepodite stages. Therefore, in summer the growth of copepods may be governed by a very low food concentration which could result in a generation time of about 40 days (Fig. 5), just like in spring. The development rates determined at different temperatures and food concentrations easily support the constant generation time of 35 to 39 days as found throughout the season for Temora by McLaren (1978).

Corkett and McLaren (1970), later supported by data from Landry (1975) and Uye et al. (1983), found evidence that the parameters α and b of Bělehrádek's function are similar for egg and post-embryonal development of marine copepods if food conditions are excessive. This form of development has been called equiproportional (Corkett, 1984). The present study also indicates that these parameters do not vary significantly at different food concentrations. This could mean an important extension of the validity of Belehrádek's function to predict development rates of copepods from embryonic duration at limiting food concentrations as well as optimal food concentrations. Once the parameter a has been determined for each food condition at any single temperature, the other 2 parameters derived from egg development at different temperatures enable one to calculate the development rate at the other food conditions at different temperatures.

The Bělehrádek's functions fitted at excess food differed greatly from the equation given by McLaren (1978) for Temora (Table III). As discussed before the rate of development may have been overestimated at low temperatures and low food levels. The consequently longer generation time at low temperatures would imply even more strongly curved Bělehrádek's functions and, hence, a still greater departure from the regression found by McLaren (1978). He obtained the value - 2.05 of parameter b from egg hatching-times of various copepod species. This common b and the value of $\alpha = -10.4$ derived from it for Temora, appeared to be valid for post-embryonal development as well (Corkett and McLaren, 1970). Using a generation time of 27.7 days observed at 12.5°C for Temora by Harris and Paffenhofer (1976b) McLaren solved the third parameter in Bělehrádek's equation and found $a = 16988$ (Table III).

The present results of Temora were obtained from direct measurements of development time at different temperatures. Since the 3 parameters of this function are dependent on each other, we also calculated α and a at food level 1, assuming b = -2.05 of McLaren. Indeed the resulting α = -11.7 and a = 18091 show much more resemblance to the values of McLaren. However, the resulting curve only fitted poorly to the measured development times; also at food level 1/16 and 1/4 a poor fit was found when *b* was assumed to be -2.05. Therefore, and since at different food levels *b* did not differ significantly, a stronger curvature seems to be realistic for our copepod population.

Prior to the start of our experiments Temora had been grown for at least 8 generations at standard conditions of 15°C. Since seasonal acclimation effects can be carried through an entire generation (Landry, 1975) it is possible that adaptation to the previous cultivation temperature has influenced the results at other temperatures. Although adaptation may have affected his experiments similarly, McLaren (1966) and McLaren et al. (1969) suggest that thermal acclimation will only take effect in the parameter α. If this is true the different values of *b* may point to fundamental physiological differences between different populations of Temora. This is in contrast with the observation of McLaren et al. (1969) that *b* is constant within closely related species.

In view of the similarity between the parameters α and *b* of egg and post-embryonal development (Corkett and McLaren, 1970), it would be interesting to measure the rate of egg development of our Temora population to see whether population differences are really involved.

Table IV. *Average mortality rate (Z) per day of Temora longicornis in 4 replicate cultures at different temperatures and food concentrations. Each + indicates the premature extermination of a culture, hence its value not incorporated in the mean value.*

Food Level	**Temperature °C**			
	5	10	15	20
0	0.046+	0.080	0.093	0.159++
1/16	0.041	0.033	0.040	0.111
1/4	0.030	0.026	0.039	0.112
1	0.021	0.030	0.034	0.104

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PHYSIOLOGICAL METHODS FOR DETERMINING COPEPOD PRODUCTION

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Abstract: Daily increments of growth, P/B, for individual communities of zooplankton or are often calculated from previously derived models of metabolism and growth efficiency. Growth P was calculated from experiments with zooplankton assemblages feeding on natural particulate matter and laboratory determined respiration and excretion rates. Experiments were carried out over more than a year in Bedford Basin, Nova Scotia, and on several cruises in other Canadian and tropical waters. Positive carbon or nitrogen balance occurred in fewer than 50% of the experiments in all locations, usually during periods of high primary production. P/B ratios in Bedford Basin during the spring bloom were 0.053±0.038 for carbon and 0.071±0.045 for nitrogen but only 0.018±0.008 for the few positive experiments at other seasons. Demographic information from the same environment suggests a higher daily P/B in summer compared with the cooler spring period. Problems with field determination of material and energy balance are discussed and some alternative *in situ* methods examined.

INTRODUCTION

Determination of rates of secondary production in the pelagic community is generally a formidable task. No practical "instantaneous" method, such as the use of a suitable radioactive tracer, has as yet been published, although Russian workers have been experimenting with such methods for some time (i.e. Shushkina et al., 1974). We might define secondary production as a total amount of primary production which is transformed through herbivory to a trophic state such that it is available for conversion through carnivory to the next trophic state; then, to measure it we need to know how much is present, how fast it grows, including that which may be converted to reproductive products, cast exoskeletons, and the like, and how much is lost to mortality from whatever cause. If a species reproduces periodically and the fate of a cohort can be followed in detail, the area under the curve relating the number of survivors at increasing time intervals to their average growth or weight increase for each interval is the production for the cohort.

Unfortunately, zooplankton often reproduce sporadically or continuously and the notoriously dynamic nature of the pelagic zone which they inhabit generally complicates the continuous observation of a cohort should one be identified. Consequently, a number of alternative methods of measuring production, usually based on determining a specific growth rate or turnover rate (production over biomass or P/B), have been devised.

In this paper we will concentrate on the applications of so-called physiological methods of obtaining an estimate of P/B, using data gathered from Bedford Basin, Nova Scotia, Canada over a period of years by a number of investigators. The environment, shown in Figure 1, is a small (17 km^2), relatively deep (70 m) marine basin connected to the Atlantic Ocean by a narrow channel with a 20 m sill. Hopefully, in such an environment with a relatively low flushing rate (Platt and Conover, 1971), the

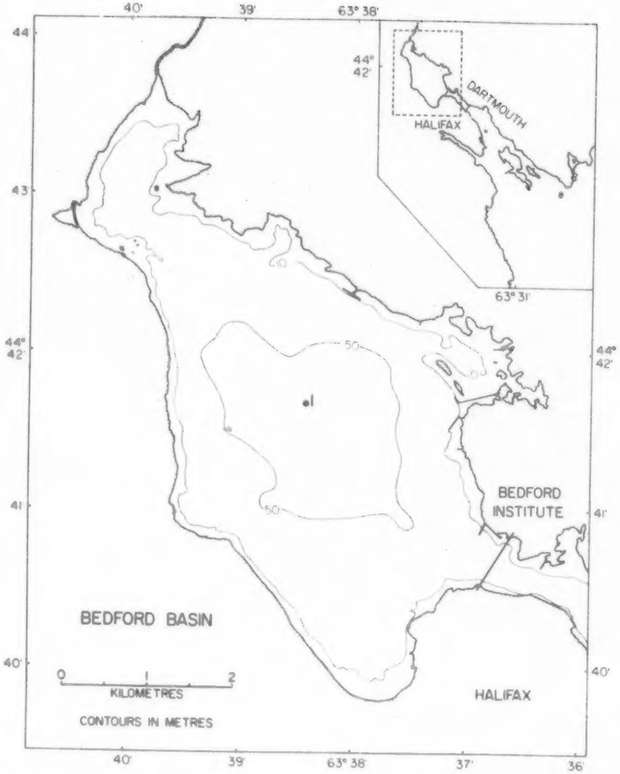
40'
39'
63° 38'
44
43
44°
42'
41
40'
DARTMOUTH
HALIFAX
63° 31'
BEDFORD
INSTITUTE
50
1
BEDFORD BASIN
0
1
2
KILOMETRES
CONTOURS IN METRES
HALIFAX
37'
36'

Figure 1. *Bedford Basin showing the station most frequently sampled.*

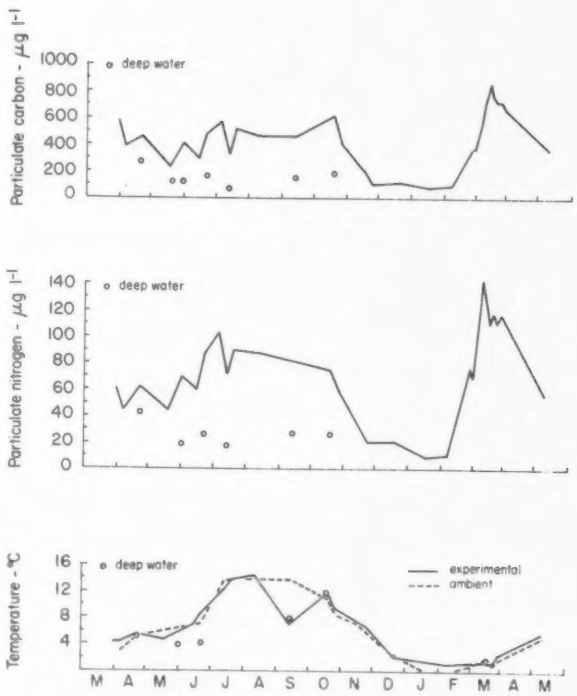

Figure 2. *Seasonal distribution of particulate carbon (upper), particulate nitrogen (middle), and temperature (lower) in Bedford Basin in the euphotic zone (5-10 m) and at 30 m (deep water) between March 30, 1976 and May 9, 1977.*

integrity of the zooplankton community over time should facilitate estimation of zooplankton production by demographic techniques (McLaren and Corkett, 1981) enabling us to make realistic comparisons between methods.

THE BASIC PRODUCTION MODEL

Any method of determining how much more a group of organisms assimilates from their environment than they require for physiological homeostasis can yield a physiological estimate of production. The term was probably first used by Winberg (1966) and the model which he developed was adapted for use in zooplankton studies by Shushkina (1968). If production (P) represents growth per unit time and M, the metabolic loss of energy in the same units as P, then the coefficient of utilization of assimilated food energy for growth, sometimes called net growth efficiency,

$$K_2 = P/P + M \qquad (1$$

and so

$$P = MK_2/1\text{-}K_2. \qquad (2$$

In its original conception M was derived from the familiar allometric relationship for metabolic rate so that

$$P = M_1 w^{\gamma} K_2/1\text{-}K_2 \qquad (3$$

where w is the mass or energy of an organism and M_1 and γ are constants.

Taking

$$N = M_1 K_2/1\text{-}K_2,$$

then

$$P = Nw^{\gamma}. \qquad (4$$

Assuming growth to be effectively parabolic, K_2 should be constant and then the weight specific growth rate

$$C_w = P/B = dw/wdt = P_w^{-(1-\gamma)}. \qquad (5$$

Individual short term productivities for different size classes or stages of zooplankton can be summed to give a population production P_p such that

$$P_p = \sum_{i=o}^{i=D_m} C_{wi} n_i w_i \qquad (6$$

where D_m is the development time for the oldest stage (generation time), n_i is the number of animals of age i, and w_i their mean weight.

The problem with this type of treatment is that K_2, M_1 and γ are not necessarily constant and may vary with food quantity and quality, temperature and probably other environmental variables.

For Bedford Basin, we have derived empirical expressions to determine respiration, excretion, and ingestion from which we hoped to be able to calculate the carbon and nitrogen balance for the zooplankton community at any time of year and, hence, the necessary P/B ratios to calculate annual production.

BEDFORD BASIN EQUATIONS

Respiration and excretion measurements are described in Conover and Mayzaud (1976). Two equations determined by step-wise multiple regression from a year's data gathered in 1974-1975 (Table 1 in Conover and Mayzaud, 1976) have been utilized to calculate metabolic expenditure. Weight specific Respiration 1 (R_1') depends only on the weight of the organisms (w) and their environmental temperature (T), while Respiration 2 (R_2') also incorporates information on particle volume (PV) in the environment as a measure of potential food supply. In addition we adapted an equation from Ikeda and Motoda (1978), based on information gathered over a wider range of boreal conditions, to give an estimate Respiration 3 (R_3'). All three equations are shown in Table 1. To convert R_1' to carbon metabolised M, a respiratory coefficient of 0.8 was assumed.

Several equations were used for estimation of ammonia excretion. Ex_1' was taken directly from Table 1 of Conover and Mayzaud (1976) and, because we did not measure exactly the same independent variables in later surveys, we also recalculated an equation for Ex_2' in order to incorporate total particulate volume (PV) and total particulate nitrogen (PN) (Conover and Mayzaud, unpublished data). We used as Ex_3' a modification of an excretion equation from Ikeda and Motoda (1978). Again all equations appear in Table 1.

Ingestion rates were studied on 29 sampling dates between March 30, 1976 and May 9, 1977. Grazing and assimilation were measured by methods described in Conover and Mayzaud (1984). In the same experiment, particle volume was determined with a Model T Coulter Counter and particulate carbon and nitrogen in water and animals were measured with a Hewlett Packard 185B C-H-N analyzer. Stepwise multiple regression was again used to examine the effect of various combinations of independent variables on the dependent variables, ingestion and filtration rate.

Three equations for ingestion were generated: Ingestion 1 (I_1') with the dependent variable carbon consumed (C); I_2', with particle volume consumed (mm^3) dependent, and I_3' in which nitrogen ingestion (N) was dependent (Table 1). To convert ingestion in terms of particle volume (I_2') to μgC, a regression equation

$$PC = 87.272\ PV + 135.0, \qquad (16$$

based on 248 paired values ($r^2 = 0.916$) from Bedford Basin and nearby coastal waters, was used.

Absorption (assimilation) was measured as shown in Conover and Mayzaud (1984) for both carbon and nitrogen. In the case of carbon there was a slight but significant positive regression against particle volume or particulate carbon in the environment with 44 pairs of data in the analysis, although only about 12% of the variability was thus explained.Even so we used the equation

$$PC_{ABS} = 0.473\ PV + 56.6 \qquad (17$$

to calculate carbon absorption in the model. For nitrogen absorption there was no significant slope so that the average intercept, 62%, was used.

The growth efficiency (coefficient of utilization of assimilated food energy for growth) was determined as

$$KC_2 \text{ or } KN_2 = \frac{I_1\ (\%ABS) - M_1}{I_1\ (\%ABS)} \qquad (18$$

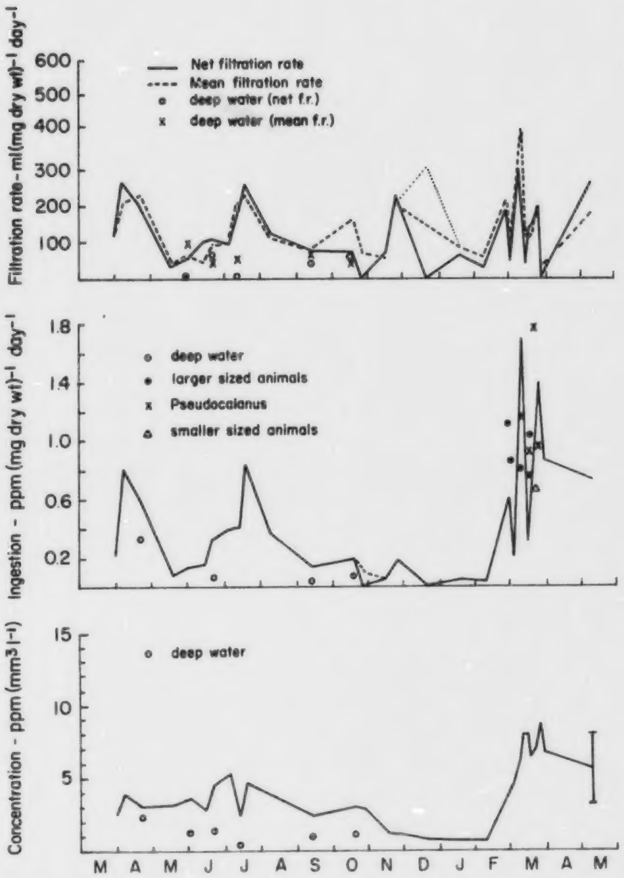

Figure 3. *Filtration rate (upper) and ingestion rate (middle) for the Bedford Basin zooplankton community in the euphotic zone (5-10 m) and deep water (30 m) and the seasonal distribution of particle volume (lower) in ppm (mm^3l^{-1}) at two depths between March 30, 1976 and May 9, 1977. Net filtration rate is based on changes in total particle volume. Mean filtration rate is the average of both positive and negative values for each Coulter Counter channel.*

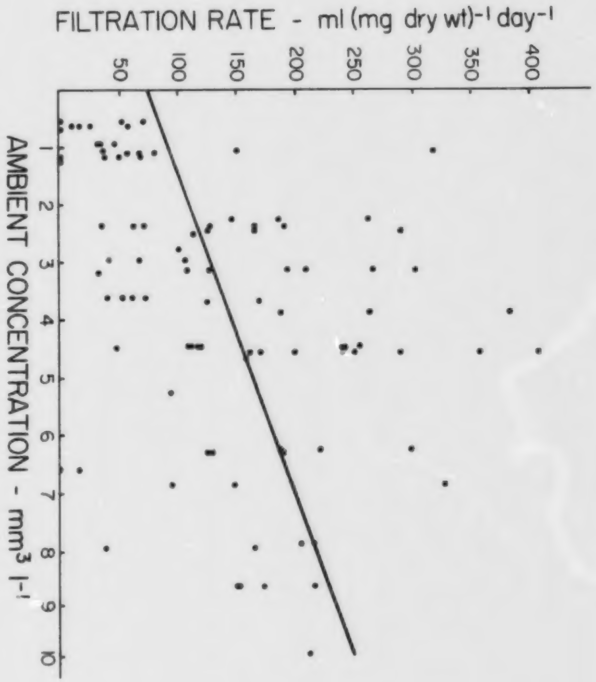

Figure 4. *Relationship between filtration rate in ml (mg dry weight)$^{-1}$day^{-1}, for all animal communities combined and the ambient particle volume.*

SEASONAL BEHAVIOUR OF INDEPENDENT VARIABLES

The pattern of production in Bedford Basin would seem to be typical for boreal neritic waters. The biological year usually begins in late winter with the onset of the spring diatom bloom, which normally peaks in March and dies away in April and May. In 1976-1977 particulate concentrations increased again in June and remained relatively high into October with only a minor suggestion of a fall bloom (Figs. 2 and 3). A distinct fall bloom has been observed in other years, however (Conover and Mayzaud, 1976; Sinclair et al., 1981). Summer-fall phytoplankton is dominated by flagellates. In the euphotic zone the annual temperature range is about 12-14°C (Fig. 2).

SEASONAL BEHAVIOUR OF DEPENDENT VARIABLES

Both filtration and ingestion rates are high in spring during the coldest part of the year and show additional peaks at several times over the productive season (Fig. 3). Indeed both filtration and ingestion rates are highly correlated with particulate concentrations in the environment (Figs. 4 and 5), but are poorly and negatively correlated with temperature (Fig. 6). Note also that there is no input by temperature in any of the three ingestion-estimating equations in marked contrast with the equations generated to predict respiration and ammonia excretion (Table 1).

OPERATION OF THE MODEL

We anticipated that three independent variables, notably body size, temperature and food supply, would contribute most of the variance to seasonal studies of zooplankton physiology in a variable environment. Accordingly we tried to generate equations by statistical means utilizing all three potential contributors of variance, so long as an additional variate was statistically supportable, even though in some cases the addition of another partial regression coefficient decreased rather than increased the value of R^2 (Table 1). Therefore, we operated the model using various combinations of the equations given in Table 1.

As shown in Fig. 7, K_2 for carbon was not constant nor indeed positive over a considerable portion of the year. Here we have utilized four combinations of the six equations. In the model R_1' and R_2' (equations 7 and 8 Table 1) give the same values for catabolism within a few percent, but these estimates were 2 to 3 times greater than those derived from R_3' (Equation 9). Ingestion 2 (Equation 14) yielded consistently higher estimates for carbon consumption than I_1' (Equation 13) because equation 16, which we used to convert particle volume to carbon, has a significant positive intercept (135). It could be argued that the combination I_1' and R_1' represent most closely the actual measured activity of Bedford Basin zooplankton and assuming that either I_2' or R_3' applied might not be entirely justifiable. Even so, without making such assumptions, almost no positive carbon growth was predictable except during the spring bloom. Although not presented here, if we use the metabolic model described to estimate nitrogen balance (K_2 for nitrogen) the pattern is virtually the same: over most of the warm months, more nitrogen, as ammonia, is metabolized and excreted, than is assimilated by the Bedford Basin zooplankton. However, over the year, a higher percentage of the experiments were in positive balance if nitrogen ingestion was the dependent variable (Table 2).

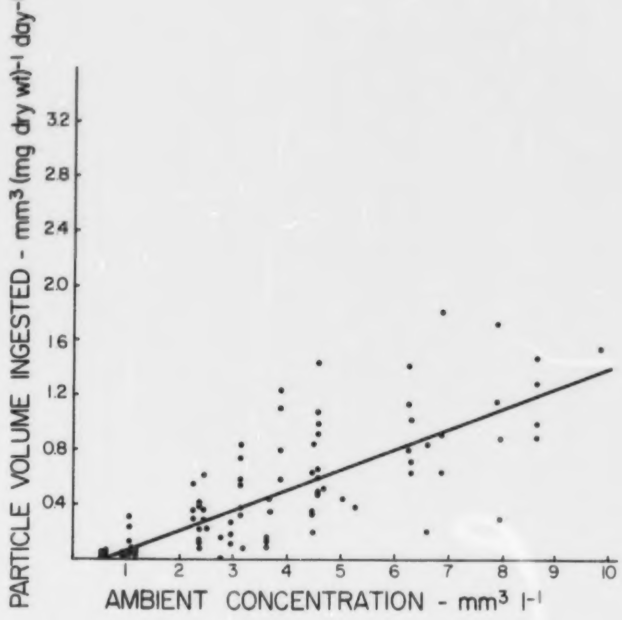

Figure 5. *Relationship between ingestion, in mm³ (mg dry weight)$^{-1}$day^{-1}, for all animal communities combined, and the ambient particle volume.*

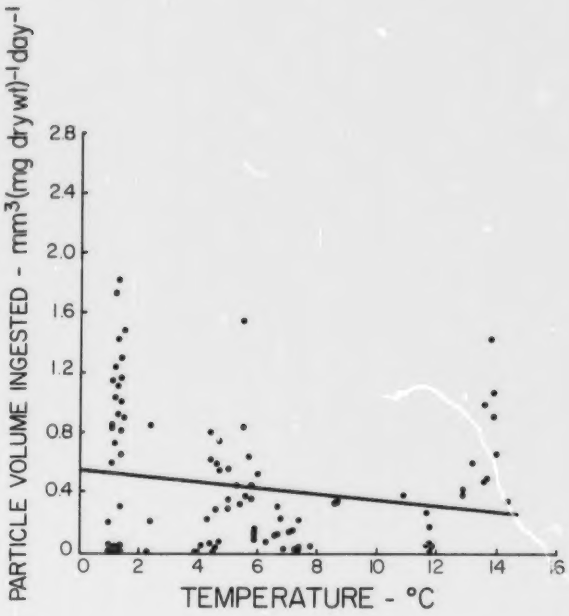

Figure 6. *Relationship between ingestion, in mm³ (mg dry weight)$^{-1}$day^{-1}, and ambient temperature in °C.*

Table 1: *Empirical equations used to calculate production in Bedford Basin by physiological methods*

Dependent variables and dimensions	Independent variables and dimensions
R_i, $\mu l\ O_2$ (animal)$^{-1}$ time^{-1}	w, dry weight of animal in micrograms (μg)
R_i, $\mu l\ O_2$ (mg dry weight)$^{-1}$day^{-1}	T, temperature in ^oC
Ex_i, μg ammonia N (animal)$^{-1}$time^{-1}	PV, particle volume in mm³ l^{-1}
Ex_i, μg ammonia N (mg dry weight)$^{-1}$day^{-1}	PN, total particulate nitrogen as μg N l^{-1}
I_i, μg or mm³ (animal)$^{-1}$day^{-1}	PC, total, particulate carbon as μg C l^{-1}
I_i, μg or mm³ (mg dry weight)$^{-1}$day^{-1}	C, carbon weight of animal in μg
	N, nitrogen weight of animal in μg
	CN, carbon to nitrogen ratio of animals

	R^2	Equation No.
$\log R_1' = 0.032\ T - 0.565 \log w + 2.402$	0.476	7
$\log R_2' = 0.024\ T - 0.580 \log w + 0.166 \log PV + 2.398$	0.300	8
$\log R_3 = (-0.01089\ T + 0.8919)\log w + 0.02538\ T - 0.1259;\ R_3' = 24\ R_3\ (1000/w)$	-	9
$\log Ex_1' = 0.027\ T - 0.380 \log w + 0.851$	0.576	10
$\log Ex_2 = 0.027\ T + 0.802 \log w + 0.469 \log PV - 0.373 \log PN - 1.910;\ Ex_2' = Ex_2\ (1000/w)$	0.680	11
$\log Ex_3 = (-0.00941\ T + 0.8338)\log w + 0.02865\ T - 1.2802;\ Ex_3' = 29.14 Ex_3\ (1000/w)$	-	12
$\log I_1 = 0.725 \log PV + 2.383 \log C - 1.971 \log w + 0.393 \log PC - 1.483;\ I_1' = I_1\ (1000/w)$	0.703	13
$\log I_2' = 1.163 \log PV - 3.291 \log w + 0.277 \log C + 0.343$	0.814	14
$\log I_3 = 0.877 \log PV + 4.060 \log N + 0.296 \log PN - 3.658 \log w + 3.229 \log CN - 0.756;\ I_3' = I_3\ (1000/w)$	0.783	15

Table 2: *Percentage of positive balance experiments from several environments in different latitudes and the average daily P/B ratios calculated from them. Values in parentheses calculated from I_2 (Table 1).*

Location	Latitude	Longitude	Dependent variables	Season	No. experiments	% positive balance	Daily P/B for positive experiments	
							Mean	S. D.
Bedford Basin	$44^o41'N$	$63^o38'W$	C	Spring 1977	27	67(100)	0.053(0.224)	0.038(0.102)
			C	Rest of year	57	2(68)	0.001(0.104)	- (0.015)
			N	Spring 1977	27	100	0.071	0.045
			N	Rest of year	57	29	0.018	0.008
Scotian Shelf	44^o-45^oN	62^o-64^oW	N	April 1979	77	29	0.025	0.018
Eastern Canadian Arctic	73^o-79^oN	55^o-95^oW	C	Aug-Sept 1980	50	10	0.004	0.005
Eastern tropical Pacific	9^o-10^oN	89^o-94^oW	C	March -	45	11	0.121	0.094
			N	April, 1981	45	20	0.068	0.060

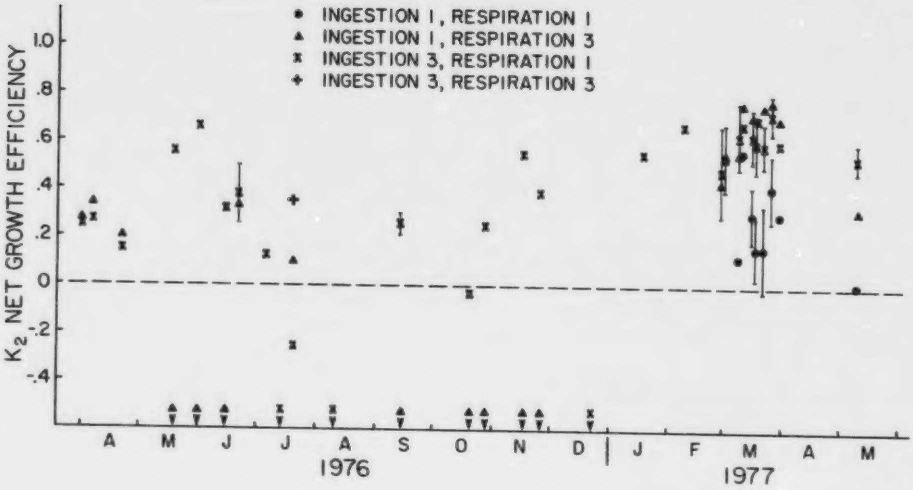

Figure 7. *Seasonal distribution of K_2 (coefficient of net growth efficiency) for Bedford Basin zooplankton communities based on equations given in Table 1 between March 30, 1976 and May 9, 1977.*

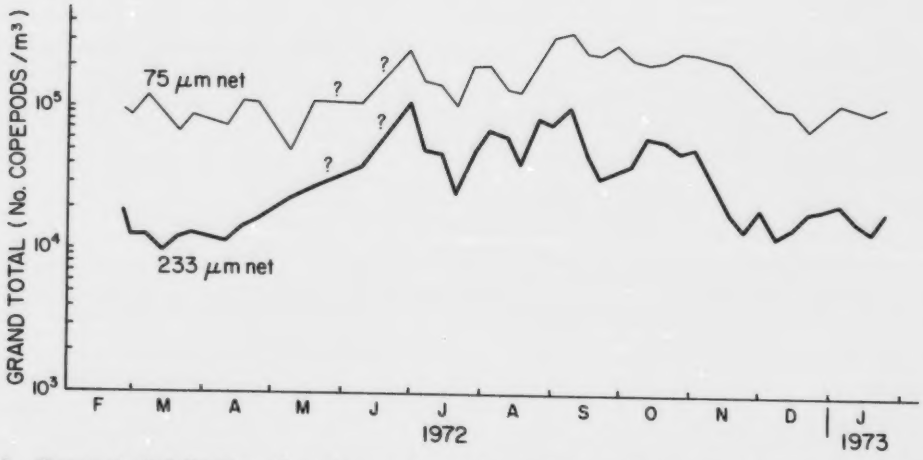

Figure 8. *Seasonal distribution of total numbers of copepods collected with nets of two different mesh sizes between February 25, 1972 and January 24, 1973. Thin line, 75 um net; heavy line, 233 um net.*

Regrettably we were unable to carry out detailed quantitive analysis of the zooplankton community structure and abundance in 1974-1975 nor in 1976-1977, when the physiological data were gathered, but such information was availabe for 1972-1973 from Bedford Basin. Figures 8 and 9 suggest that in the earlier years the number and biomass of zooplankton increased in the warm months. We have also examined the age and size structure for several important copepods in the Basin during 1972-1973, and all show production of several generations during the warm months (Fig. 10).

DISCUSSION

What has gone wrong? Were the three years over which the physiological, population and production measurements were made so different that combining them to form a predictive model was unrealistic? We do not really think that this was the major problem although in some measure it probably contributed. However, in order to eliminate such criticism a series of additional balance experiments were carried out on the Scotian Shelf, in the eastern Canadian Arctic and in waters off Central America in the eastern tropical Pacific. In these experiments, grazing and ingestion rates, respiration and excretion were all carried out simultaneously with material from the same tow, or in some cases, in the same experimental chambers. The methods used for the balance experiments are given in detail by Conover and Cota (1984).

As demonstrated by the summary Table 2, making all the physiological measurements simultaneously, or nearly so, did not improve the chances of obtaining an estimate of daily growth. The Scotian Shelf cruise was planned to coincide with the spring pulse of phytoplankton in coastal water adjacent to Bedford Basin, but our timing was not perfect. The bloom was collapsing at the start of the cruise and our percentage of sucessful experiments decreased with the decline in chlorophyll. The Arctic experiments were carried out over a wide geographic area with a wide range of ambient conditions in the water column, and again positive balance and higher concentration of particulate were usually positively correlated. In an earlier paper, we postulated that some of the Arctic zooplankton which we studied in late August and September, 1980, could have completed their annual feeding and growth cycle so that with the decrease in phytoplankton at the end of summer, they may already have been in the early stages of diapause (Conover and Cota, 1984). Nonetheless, some zooplankton populations, including those of Bedford Basin in summer and those in the tropical Pacific, appeared to thrive when the standing crop of potential food, as we on the surface perceived it, was not very great.

The discrepancy between zooplankton nutritional requirements and their available food supply has been recognized for at least 75 years (Pütter, 1909). More recently Mullin and Brooks (1976), using laboratory derived curves for ingestion as a function of plant carbon, concluded that there was insufficient nutriment to support Calanus pacificus growth at 40% of the points sampled, although at most stations there was some depth where the carbon budget would balance. In the shelf area off southern California, half the stations along a transect parallel to the coast contained too little plant material on average to support the resident copepods (Cox et al., 1983). Off New York Bight, Dagg and Grill (1980) found that the feeding rate for Centropages typicus was usually less than maximal.

The problems of balancing material or energy budgets in shipboard simultations of nature is further compounded by the "patchy" distributions of consumers and consumed. Whether or not phytoplankton actually "excludes" zooplankton (Hardy and Gunther, 1935), plant and animal plankton frequently do not occur in the same water parcel in similar relative concentrations. Where they do, as during bloom

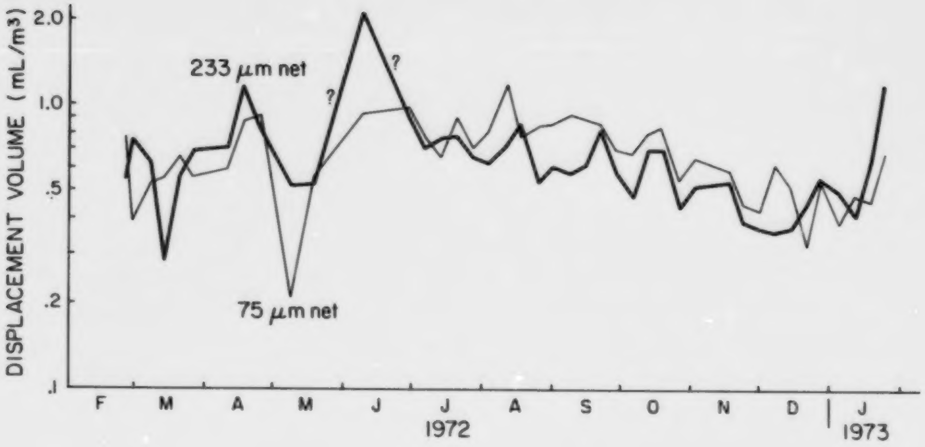

Figure 9. *Seasonal distribution of displacement volume in ml/m³ measured, using nets of two different mesh sizes, between February 25, 1972 and January 24, 1973. Thin line, 75 um net; heavy line 233 um net.*

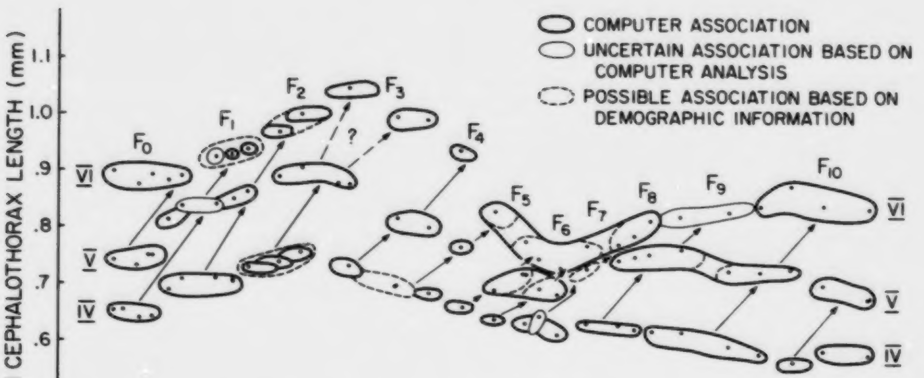

Figure 10. *Size distribution of three different stages of Pseudocalanus sp. in Bedford Basin between February 25, 1972 and January 24, 1973. Separation between generations (size groups) was based on the Student-Newman-Keuls multiple comparison test as programmed by the International Mathematical and Statistical Libraries, Inc.*

periods, it is relatively easy to demonstrate positive growth in laboratory microcosms, as we have shown (Table 2, Fig. 7, see also Taguchi and Ishii, 1972). When they do not, which is usually the case, the problem becomes exceedingly complex. In the first place, there is the well known but poorly understood phenomenon of diel vertical migration. Why should grazing animals waste all that energy swimming up and down for a few hours of grazing in the plant-rich zone when they might just as well spend their entire time where the plants are growing? We will not attempt to answer that question here, but the point is that migratory animals have only transient encounters with their food supply which is still somehow sufficient to meet their nutritional requirements. Indeed, Paffenhöfer (1976) could demonstrate no differences in total ingestion between laboratory populations of Calanus helgolandicus (probably C. pacificus) kept in continuous food or permitted to feed only at night, regardless of food concentration.

Any other pattern of distribution or behaviour, or physical phenomenon which contributes to the displacement of zooplankton from their food, makes the study of zooplankton-phytoplankton interactions more complex. Here, we could mention, endogenous-, or any other rhythmic feeding pattern occurring where plants and animals are apparently in continuous contact.

To illustrate the significance of the physical environment on zooplankton feeding, and the importance of transient food getting, we relate some still largely anecdotal observations by one of us (RJC) this past May in the Canadian Arctic. First, I should acknowledge my colleague, Alex Herman, whose under ice pumping system made these observations possible. In Barrow Strait, off Resolute Bay, NWT, there are relatively strong tidal currents even though two meters of new ice form each winter. The first manifestations of spring plant production are formed primarily by pennate diatoms on the under ice surface beginning in mid- to late April. In the upper 10 m of water just under the ice the spring copepod community is dominated by Pseudocalanus sp. which begins to show evidence of population growth just about the same time that the ice algae began to develop, although the amount of particulate matter in the water column was almost undetectable. At the same time, the guts of net caught Pseudocalanus began to show green. We found, using the under ice pump system by sampling at 10 to 25 cm intervals, that the Pseudocalanus crowded up against the ice surface during slack water to feed in unbelievable numbers (thousands per liter) but they apparently could not maintain proximity to their food-supply when the tide began to run again. So the entire population would seem to depend on 2 to 4 hours of feeding per day, on admittedly very dense food concentrations, for maintenance and what would seem to be a very high rate of population production, during the pre-open water season. Feeding rates for these under ice Pseudocalanus at -1.8°C, using melted ice algae as food, were higher than any ever measured by us for the same genus in Bedford Basin at 10 or 15°C higher temperature.

We have concentrated here to now on the problems of reliably estimating ingestion (and assimilation) in balance experiments as a means of estimating secondary production. Judging by the amount of explainable variance in our model, respiration and excretion rates were even less predictable than ingestion (Table 1). Added is the assumption that oxygen utilization tells us something about carbon oxidation. Could we measure carbon dioxide production with about the same precision as carbon ingested or nitrogen excreted, there might be hope, but to date, there have been few attempts to measure even the respriratory quotient (R. Q.) for zooplankton (Raymont and Krishnaswamy, 1968; Lampert and Bohrer, 1984). Perhaps direct calorimetry will be more useful than material exchange for measuring catabolic metabolism in zooplankton (Hammen, 1983; Knudsen et al., 1983). However, for the present, nitrogen balance seems to be easier to achieve than carbon (Table 2), but we still know virtually nothing about factors contributing to short term variability in nitrogen metabolism despite several recent advances (Gardner and Scavia, 1981; Hawkins and Keizer, 1982).

For the most part our physiological methods are simply measuring the noise in the pelagic ecosystem and, while these kinds of observations have given us information about ecosystem function, the amount of energy or carbon produced by the system over a period of months or years is the integrated sum of all these millions of confusing details. Therefore we need to measure something in the organism in the environment that relates to past history and predicts future performance. Several kinds of biochemical indicators now seem to hold great promise. Lipofuscins or "age pigments" should simplify our analysis of age structure among pelagic communities, especially for those organisms that require more than one year to complete a life cycle (Ettershank, 1983). Nucleic acid ratios may be useful growth predictors for planktonic organisms (Buckley, 1984). Enzymes of the electron transport system (ETS) hopefully integrate the previous environmental history as it affects respiratory metabolism (Bamstedt, 1980). The amount of glutamate dehydrogenase (GDH) in zooplankton may predict ammonia excretion (Bidigare, 1983; King, 1984). Certain digestive enzymes could integrate previous feeding history (Cox et al., 1983; Head et al. 1984). But still we are trying to evaluate these biochemical integrators by comparing them with our noisy physiological methods. Rather, to improve the usefulness of physiological methods as predictors of zooplankton production, we must go back to the laboratory to see how the short-cut methods relate to long-term culture and growth experiments under carefully controlled conditions.

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SYMPOSIUM ON GROWTH, LIFE AND CULTURE

Conclusion by Dr. C. HEIP

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Culturing techniques for marine copepods have advanced greatly over the last two decades, mainly in the context of ecological and genetic research; even though copepods are an excellent food source for many larval and juvenile fish, and therefore potentially useful in aquaculture, the main emphasis has been on growth, life-history and energy-flow studies.

Two field and three laboratory studies were reported in this session. Klein-Breteler studied 16 food-temperature combinations on the development of *Temora longicornis*, a North Sea species for which the field data did not permit any accurate estimate of growth-rate. Culturing was greatly facilitated by adding one trophic level, the algae-eating dinoflagellate *Oxyrrhis marina*. Development was not isochronal and slowed down about half-way, but in general the growth rate increased with increases in food and temperature.

The effects of food and temperature were also taken into account in the regression equations presented by Conover and Poulet relating ingestion, respiration and excretion to weight, temperature and food concentration. These equations may have an important use, as many instances they are the only possible means to arrive at estimates on the energy flow through calanoid copepods when only field data are available. However, the situation is very complex and though the authors appear to be too pessimistic when stating that we are only measuring the noise in the system, these are real problems. Variability in these (and many other) laboratory measurements is very large, there are seasonal differences, there are differences in P/B or net growth efficiency measures whether they are based on C or on N, etc. Some alternative routes may be explored: age pigments, nucleic acid ratios, ETS, dehydrogenase-activity and ohters were suggested.

Some warning against the over-enthusiastic use of laboratory measurements is indeed warranted. Heip's study shows the great importance of long term variability in the temporal domain, whereas Davis' study shows the same for the spatial domain. On Georges Bank large spatial differences exist in the age-structure of the calanoids which depend on the circulation pattern of the water on the Bank. *Pseudocalanus* and *Paracalanus* do not appear to be food-limited at all but are probably regulated by temperature and predation. Predation has been shown to be an important generator of cyclicity in the benthic harpacticoids studied by Heip, yet it is rarely studied let alone quantified in the laboratory.

This is not to say that food is unimportant; it may limit *Calanus finmarchicus* on Georges Bank, and Connover and Poulet show that *Pseudocalanus* does not grow well unless high concentrations of phytoplankton are present. It is important to study the effect of food at concentrations found in nature. Paffenhöfer's study is aimed at this and was furthermore important in showing that calanoids may 'taste' and accept or reject particles, and to accept them slower or faster according to size and composition. Many of our ideas concerning feeding of calanoids may undergo drastic changes and the cinematographic techniques as used by Paffenhöfer will become increasingly important.

That copepods are not necessarily stupid (though beautiful) machines make their study all the more difficult. Good descriptive and experimental ecological and taxonomical work remains necessary; laboratory experiments should always bear the ecological and evolutionary context of species in mind when they are used to explain or predict the behaviour of real ecosystems.

3. Biogeography (Chairman: *J.-s. Ho*)

LONGITUDINAL DISTRIBUTION OF OCEANIC CALANOIDS (CRUSTACEA: COPEPODA): AN EXAMPLE OF MARINE BIOGEOGRAPHY

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Abstract: Distribution of marine calanoids is reviewed, with an emphasis on the distribution patterns of morphologically similar species within an ocean and in different oceans.

INTRODUCTION

Calanoid copepods are the dominant group of marine zooplankton both by number of species and by quantity of biomass. The first marine calanoid to be named was Calanus finmarchicus, described as Monoculus finmarchicus by Gunnerus in 1770, not long after the publication of the tenth edition of Linnaeus's Systema Naturae. New marine calanoids were sporadically reported during the next eight decades. Prior to the first major contribution to calanoid taxonomy by Dana (1849), only nine species of marine calanoids in seven genera had been described.

There are two prolific periods in the history of calanoid taxonomy (Fig. 1). The first is a 30-year period before World War I when many marine biological stations were established and some primary oceanographic expeditions took place. By the end of this period, about 600 species of marine calanoids in 100 genera were known to science and the wide distributional range of some of these species had already been noted.

The second period, also of 30 years, immediately follows World War II. This is a period marked by numerous comprehensive oceanographic surveys carried out by individual institutions as well as international cooperative projects. Systematic studies based on world-wide material collected from multiple adjacent stations have eliminated some previous taxonomical confusion and produced additional insight on the biogeography of marine calanoids. By the end of this period, the number of known marine calanoids had been increased to approximately 1,200 species in 150 genera.

Marine zooplankton are characterized by their small number of species and wide range of species distribution. Although many of the so-called cosmopolitan species of marine zooplankton reported in the older literature have been proven to contain a number of morphologically similar species with different ranges of geographical distribution, more than 60 % of marine planktonic animals are still considered to be either cosmopolitan or widely distributed between latitudes 50^{o}N and 50^{o}S (Van Soest, 1979).

The latitudinal or north-south pattern of species distribution has long been the focus of attention of biogeographers. Marine biogeographers of the late nineteenth and early eighteenth centuries believed that the pattern of latitudinal distribution of marine zooplankton was in accord with the temperature regimes of the sea. With the advancement of physical oceanography and the availability of comprehensive biological collections since the end of World War II, it has become apparent that the latitudinal distribution of marine zooplankton is highly correlated with hydrographical features of the ocean, such

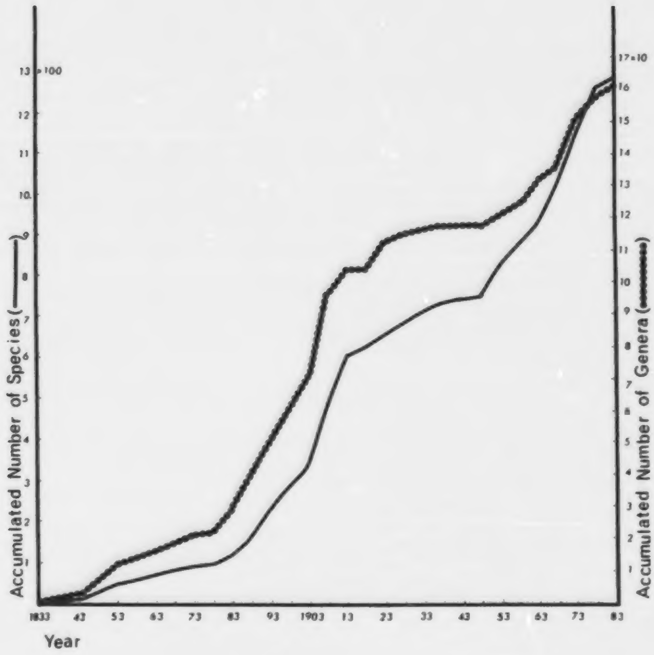

Figure 1. *Accumulation of number of described species (line) and genera (beads) of marine calanoids from 1770 to 1983.*

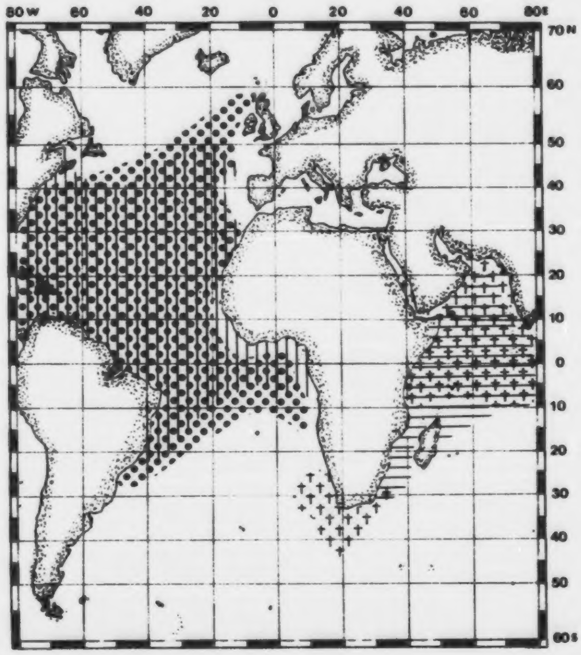

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Figure 2. *Distribution of Rhincalanus cornutus (vertical bars), R. rostrifrons (crosses), and Atlantic form (dots) and Pacific form (horizontal bars) of Candacia pachydactyla in the Atlantic and Indian oceans (redrawn from Shih, 1979).*

as water masses, gyre motion, and current system (see reviews by McGowan, 1971 and Dunbar, 1979).

The longitudinal or east-west pattern of species distribution in marine zooplankton has been ignored by most biogeographers. This report, by using examples of calanoid species reported in the literature, reviews the general pattern of longitudinal distribution of morphologically similar species and explores the significance of this type of distribution in marine biogeography.

LONGITUDINAL DISTRIBUTION

Examination of widely distributed species of marine zooplankton frequently leads to the discovery of two or more morphological forms, usually occuring within the same latitudinal range but in different parts of the world ocean. As a result, these morphological forms are sometimes taxonomically split;they are hereinafter termed "analogous species". There are two basic types of analogous species: interoceanic and intraoceanic.

Interoceanic Analogous Species

Interoceanic analogous species occur in different oceans and are usually widely separated. For example, they are commonly found separately in the Atlantic and Indian or the Atlantic and Pacific oceans. Morphological differences among these species are often inconspicuous but persistent. Rhincalanus cornutus Dana of the Atlantic and R. rostrifrons Dana of the Indo-Pacific had been considered as one species since Giesbrecht (1892) synonymized them. Schmaus (1917) was able to separate the female Atlantic and Indo-Pacific specimens by the 5th legs and designated forma atlantica and forma typica respectively for these two forms (Fig. 2). The Atlantic form is mainly distributed between 45°N and 15°S in the Atlantic, with some small isolated populations in the higher latitudes of the South Atlantic. The typical form occurs mainly in the tropical waters of the Indian and Pacific oceans, but is also found around the southern tip of Africa. Bowman (1971) confirmed the differences between these two forms and restored them to their original species status.

Although Candacia pachydactyla (Dana) is distributed in tropical and subtropical waters of all oceans, Jones (1966) found morphological differences in the genital segment and other structures in both sexes between Atlantic and Indian ocean specimens (Fig. 2). Moreover, there is a distributional gap between the Atlantic and the Indian ocean forms of this species which occurs around the southern tip of Africa. It thus seems very likely that these are not two forms of C. pachydactyla but instead are two separate, perhaps geminate species because the gene flow between these two forms seems to be interrupted by the large geographical gap between the two populations.

The most interesting example of interoceanic analogous species is demonstrated by the two species groups, Calanus finmarchicus (Gunnerus) and C. helgolandicus (Claus) (Fig. 3). The identity of these species had confused copepodologists for many years. They could not decide whether C. helgolandicus is different from C. finmarchicus, or wether C. helgolandicus from the North Pacific is identical to that from the North Atlantic. Our present knowledge to the taxonomy and distribution of these species is the result of a number of investigations, including Brodsky (1948, 1959), Jaschnov (1955, 1970), Frost (1971, 1974), and Fleminger and Hulseman (1977). Presently the finmarchicus species group contains C. finmarchicus in the North Atlantic, C. glacialis Jaschnov in the Arctic and northern parts of North Atlantic and North Pacific, and C. marshallae Frost in the North Pacific with a few stray

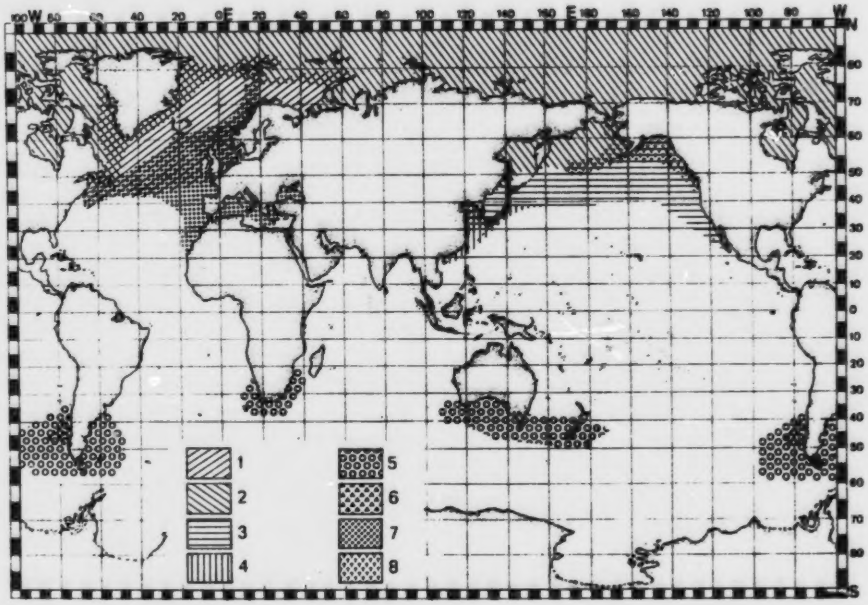

Figure 3. *Distribution of the species of Calanus finmarchicus and C. helgolandicus species groups (modified from Shih, 1979):*
C. finmarchicus species group: 1. C. finmarchicus; 2. C. glacialis; 8. C. marshallae. C. helgolandicus species group: 7. C. helgolandicus; 3. C. pacificus; 4. C. sinicus; 5. C. australis; 6. C. chilensis.

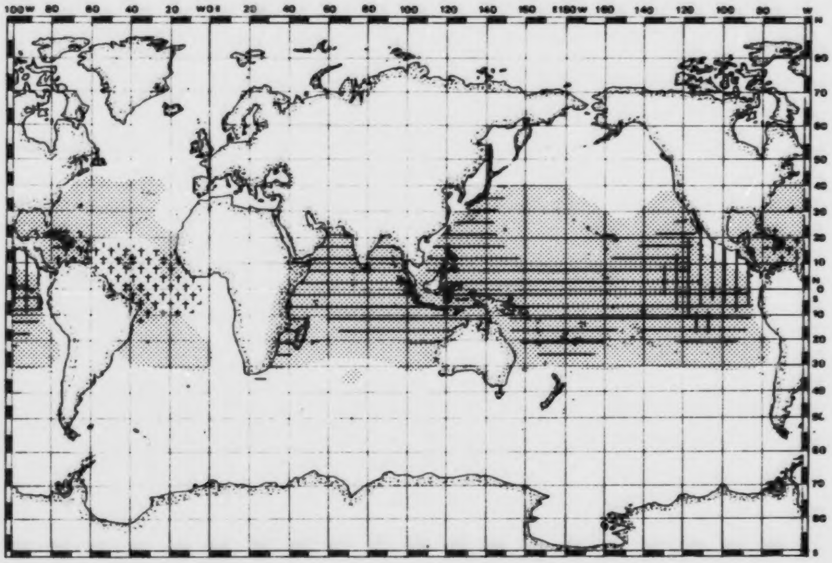

Figure 4. *Distribution of the species of Pontellina (modified from Fleminger and Hulsemann; 1974): P. plumata (dots), P. morii (horizontal bars), P. sobrina (vertical bars), and C. platychela (crosses).*

records from the Canadian Arctic. Members of the helgolandicus species group now include C. helgolandicus in the North Atlantic, C. pacificus Brodsky and C. australis Brodsky in the Southern Ocean. These species of Calanus can be distinguished by the curvature and size of dentition on the inner margin of the first basipodite of the 5th legs in females, by the proportion of different segments in the 5th legs in males, and also by the configuration of integumental organs, especially those on the genital segment.

Intraoceanic Analogous Species

Intraoceanic analogous species occur in the same ocean often within the same latitudes, and there is sometimes an overlapping of distribution of these species. Morphological intergrades of forms may be present in the overlapping area. More examples of intraoceanic analogous species are reported from the Pacific than from the Atlantic. In the Atlantic, we may consider Calanus finmarchicus and C. helgolandicus as a pair of analogous species. Pontellina plumata (Dana) and P. platychela Fleminger et Hulsemann are another example and will be mentioned again later.

In the Pacific, sometimes two or three analogous species are found separately or partially overlapping in the eastern part of the ocean. Usually one of these species is limited to the eastern Pacific, and the others have wide distributional ranges covering tropical and subtropical waters of the Indian and Pacific oceans.

The warm water genus Pontellina was thought to comprise a single species, P. plumata, with world-wide distribution. But Fleminger and Hulsemann (1974) described three new species: P. platychela, P. morii, and P. sobrina (Fig. 4). In the Pacific and Indian oceans, P. plumata almost completely overlaps the distribution of congeners P. morii and P. sobrina. P. sobrina is limited to the eastern Pacific while P. morii is found in Indian Ocean, western and central Pacific and slightly overlapping P. sobrina in the eastern Pacific. In the Atlantic Ocean, P. plumata is distributed between 43°N and 37°S, but is replaced by P. platychela in the equatorial region.

Clausocalanus jobei Frost et Fleminger strongly resembles C. farrani Sewell and has been misidentified as the latter species (Frost and Fleminger, 1968). They are both warm water species and morphologically may be separated by the different shape of the rostrum in lateral view in females and the armature of the terminal segment of the 5th legs in males. C. jobei is mainly distributed in the eastern Pacific, with some isolated populations in the western Pacific, Indian, and Atlantic oceans. C. farrani occurs widely in the Indian and Pacific oceans, roughly between 30°N and 30°S, and in the eastern portion of its distributional range overlaps with C. jobei (Fig. 5).

BIOGEOGRAPHICAL GENERALIZATION OF LONGITUDINAL ANALOGOUS SPECIES

In addition to the above mentioned oceanic calanoids, longitudinal inter- and intraoceanic analogous species are also found in many other groups of marine zooplankton, for example, amphipods (Shih, 1969), decapods (Judkins, 1978), pteropods (McGowan, 1963, Van der Spoel, 1967), chaetognaths (Bieri, 1959, Pierrot-Bults, 1974), and salps (Van Soest, 1974a, 1974b). These longitudinal analogous species are usually epipelagic. They are either found within the upper 200 to 300 m of the ocean or have their center of abundance in this epipelagic layer. All except a few species (for example, all species of the genus Calanus) are warm water species inhabiting Equatorial and Central Water masses.

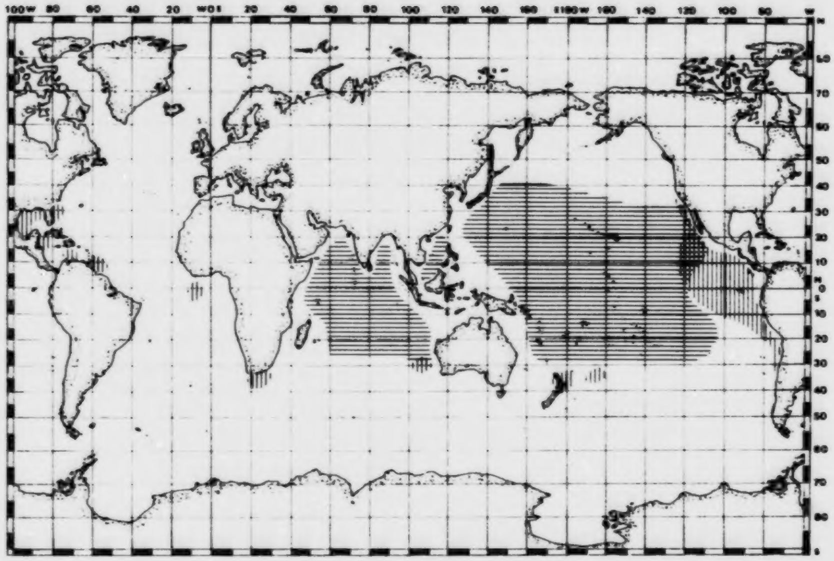

Figure 5. *Distribution of Clausocalanus farrani (horizontal bars) and C. jobei (vertical bars) (modified from Frost and Fleminger, 1968).*

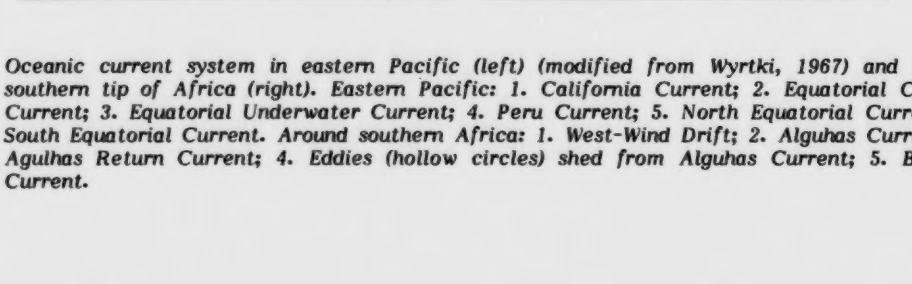

Figure 6. *Oceanic current system in eastern Pacific (left) (modified from Wyrtki, 1967) and around southern tip of Africa (right). Eastern Pacific: 1. California Current; 2. Equatorial Counter Current; 3. Equatorial Underwater Current; 4. Peru Current; 5. North Equatorial Current; 6. South Equatorial Current. Around southern Africa: 1. West-Wind Drift; 2. Alguhas Current; 3. Agulhas Return Current; 4. Eddies (hollow circles) shed from Alguhas Current; 5. Bengula Current.*

Land masses seem to be the most effective geographical barriers to longitudinal interoceanic analogous species. All analogous species pairs of the Atlantic and Pacific (except those of the *Calanus finmarchicus* species group) are widely separated by the American continents. The African continent alone may not be an effective land barrier to the analogous species pairs of the Atlantic and Indian oceans. However, the oceanic circulation around the southern tip of the continent reinforces the blockage of gene flow between the Atlantic and Indian ocean populations (Fig. 6).

The major current south of Africa is the circumglobal West Wind Drift. The West Wind Drift meets the Agulhas Current, the western boundary current of the southern Indian Ocean, at the southern tip of Africa. The Agulhas Current travels southward along Africa through the Mozambique Channel between the continent and Madagascar, coming nearest to the African shore between Durban and Port Elizabeth. This is the area where the most southerly records of *Candacia pachydactyla* (Indian Ocean form), and other longitudinal analogous species such as the amphipod *Phronima bucephala* Giles (Shih, 1969, as Indo-W. Pacific form of *P. colletti* Bovallius) and the chaetognath *Sagitta pacifica* Tokioka (Pierrot-Bults, 1974) were reported from the western Indian Ocean. On reaching the Agulhas Bank south of Cape Agulhas the Agulhas Current turns eastward in a sharp anticyclonic eddy and forms the Agulhas Return Current. These two currents also form a large elongated Agulhas eddy wedged between the continent and the West Wind Drift. Smaller eddies are frequently shed from the main stream of this current system and drift westward to the Atlantic Ocean (Wyrtki, 1973). Some interoceanic analogous species, such as *Rhincalanus rostrifrons*, are carried by these eddies from the Indian to South Atlantic Ocean. However, further drifting of these species into the Atlantic Ocean is blocked by the northward cold water current, the Benguela Current, along the west coast of Africa.

The distributional pattern of longitudinal intraoceanic analogous species seems to be strongly influenced by the oceanic current system. The best examples are found in the species pairs occurring in the eastern Pacific, such as *Pontellina morii* and *P. sobrina*, and *Clausocalanus jobei* and *C. farrani* mentioned above.

Analogous species pairs with similar distributional patterns in the same area are also present in other groups of marine zooplankton, including amphipods, euphausiids, decapods, and chaetognaths (see review by Shih, 1979). In these species pairs, one species is limited to the eastern Pacific between Baja California and Peru, and the other has a wide distributional range in the Pacific and Indian oceans, with a certain degree of overlap with its paired species in the eastern Pacific.

The current system is complicated in the eastern Pacific where these analogous species pairs occur (Fig. 6). Four currents (southward California Current, northward Peru Current, and eastward Equatorial Counter Current and Equatorial Underwater Current) converge on and two currents (westward North and South Equatorial Currents) diverge from this area (Wyrtki, 1967). The four converging currents change their course between 20°N and 10°S according to the season and feed to the westward diverging currents. Thus species from the Indo-West Pacific may be carried to the eastern Pacific by the eastward currents, e. g., the Equatorial Counter Current, or the opposite may occur via the Equatorial currents.

PERSPECTIVES IN MARINE BIOGEOGRAPHY

The world ocean has a long history of more than 2.5 b. y. (Schopf, 1980). The separation of the present oceans took place relatively recently (Herman, 1979). The Indian and Atlantic oceans were separated by the narrowing of the eastern and western ends of the Tethys Sea (of which the present Mediterranean Sea is a remnant) in the Miocene (about 10-7.5 m. y. BP). The isolation of the Atlantic from the Pacific Ocean was first established when the isthmus of Panama emerged completely in the Plio-Pleistocene (3.5-3.0 m. y. BP). The Indian and Pacific oceans have always been contiguous, although the shallow shelf region of the eastern Indian Ocean may have acted as a partial barrier to epipelagic species. During the Plio-Pleistocene Ice Age repeated periods of expansion of the cold water fauna into lower latitudes were separated by mild intervals when warm water species invaded the high latitudes. One consequence of this may be the low diversity of marine zooplankton, which is probably caused by the recent and incomplete separation of the parts of the world ocean. The longitudinal distribution of interoceanic analogous species, e. g., Calanus helgolandicus and C. pacificus, is mainly a result of isolation by land masses, but sometimes may also be partly due to the current system as seen, for instance, in Candacia pachydactyla.

In the absence of apparent geographical barriers, current and other hydrographic features of the ocean, though not very effective, seem to be acting as isolating mechanism in the process of speciation in intraoceanic analogous species.

As the population of a species from the upstream area of distribution is brought by the current to the downstream area outside the general distributional range of the species, the individuals of the population are physiologically stressed by the change in physical and biological conditions in the new environment. This may result in a change of genetical composition in the population. The expatriated population in most cases will probably not be able to overcome the environmental changes and will therefore fail to establish itself in the new environment. A good example is exhibited by the euphausiid Nematoscelis megalops (Hansen) from the Slope Water of the western North Atlantic. Occasionally a population of this species is trapped in a Gulf Stream cold core ring and transported to the Sargasso Sea. Wiebe and Boyd (1978) showed that an expatriated population of this euphausiid species became continuously more degraded and, finally, extinct while the cold core ring travelled further to the Sargasso Sea. It is however not entirely unlikely that during the long history of a species, a genetically altered population may occasionally be able to adapt to the new environment. This is postulated as one of the reasons that many pairs of analogous species are found in the eastern Pacific.

Our knowledge of the general biogeography of the plankton in the seas is restricted mainly to warm water and epipelagic species. Beklemishev (1971) emphasized that the study of marine biogeography should be carried out on a community basis. Yet, the paucity of information on deep water plankton remains a severe handicap to such community studies. Many planktonic species are known to perform diurnal migration and some may travel vertically several hundred metres daily. If the surface water masses are so effective in limiting the dispersal of plankton horizontally, why can the same animals tolerate the rapid and consistent change of environment during their diurnal migration?

The future advancement of biogeography of marine zooplankton thus must rely not only on mapping the distribution of species but also on understanding the physiological adaptation of these animals to slow and gradual (as drifting from one water mass to the other) and rapid and rhythmic (as in diurnal migration) environmental changes.

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BIOGEOGRAPHIC TRENDS WITHIN THE FRESHWATER CANTHOCAMPTIDAE (HARPACTICOIDA)

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Abstract: The family Canthocamptidae contains most of the world's freshwater harpacticoid genera. It is world wide in its distribution and its members are to be found in almost every available habitat type. The distribution of most of the genera (and certain subgenera) is dicussed. In most cases these show a restricted range and several distinct geographical groupings can be made, providing leads to the evlolutionary history of the family.

Most of the world's freshwater harpacticoid genera are included within the family Canthocamptidae which is, however, not exclusively freshwater in its distribution. There are a few genera and species which inhabit the sea, freshened parts of the marine littoral and saline inland waters. Not only is the family world-wide in its distribution, but, unlike the other major family with many freshwater species, the Parastenocarididae, its members have come to occupy almost every available niche - open water, littoral, subterranean, phytotelmic, forest moss, damp litter and soil and even to the extremely harsh environment of hot springs.

Various authors have discussed the geographical distribution of members of the family but efforts have been, and continue to be hampered by the lack of data from certain areas of the world. In his 1929 paper, Chappuis obviously then appreciated the fact that certain genera and subgenera showed restricted ranges. Other early discussions of major note on distribution include those of Brehm (1936), Lang (1948), Borutsky (1952) and Sewell (1956).

Bearing in mind our lack of knowledge of certain areas of the world and the need for a close look at certain generic distinctions (some demarcations are not very clear), the following table, Table 1, has been constructed, indicating the major areas of distribution of the freshwater genera within the Canthocamptidae, with a very rough approximation of species numbers within each category. The zoogeographical regions used are defined underneath, and close areal groupings of genera are indicated by the designation of blocks.

Obviously then, the Holarctic, more particularly the Palaearctic, contains the majority of genera and species. Genera common to both Europe and North America include *Bryocamptus*, *Canthocamptus*, *Moraria*, *Paracamptus* and the subgenera *Mrazekiella*, *Ryloviella* and *Attheyella* s.str. within the genus *Attheyella*. Those which appear to be Palaearctic restricted include *Spelaeocamptus*, *Ceuthonectes*, *Antrocamptus*, *Morariopsis*, *Epactophanoides*, *Hypocamptus* and *Gulcamptus*.

Within the Palaeotropical, the Ethiopean region contains large numbers of *Elaphoidella* and *Echinocamptus*, as well as members of *Epactophanes* and *Maraenobiotus*. The only apparent endemic genus is *Afrocamptus*, described from French West Africa and closely related to *Echinocamptus*.

The closely linked Oriental areas similarly contain many *Elaphoidella* species as well as the genera *Maraenobiotus* and *Epactophanes*. Shared with the Neotropical and Australian regions is the subgenus *Chappuisiella* of *Attheyella* while the subgenus *Canthosella* is probably restricted to this area. The apparent endemic Thermomesochra is only recently described from thermal waters in Malaysia (Itô & Burton, 1980).

Table 1: *Distribution of the freshwater genera of Canthocamptidae around the world (Approximate species numbers are indicated in brackets)*

GENUS / SUBGENUS	HOLARCTIC		PALEOTROPICAL		NEO	AUS	ARCH
	PAL	NEA	ETH	ORI			
Ceuthonectes Chappuis, 1923	X (6)						
Spelaeocamptus Chappuis, 1933	X (2)						
Antrocamptus Chappuis, 1956	X (9)						
Hypocamptus Chappuis, 1929	X (2)						
Morariopsis Borutsky, 1930	X (3)						
Epactophanoides Borutsky, 1966	X (1)						
Gulcamptus Miura, 1969	X (1)						
Bryocamptus Chappuis, 1928	X (53)	X (17)		X (2?)		X (2)	
Canthocamptus Westwood, 1836	X (6)	X (7)		X ?			
Moraria T. & A. Scott, 1893	X (33)	X (6)					
Paracamptus Chappuis, 1929	X (4)	X (2)					
Attheyella Brady, 1880							
S.G. Mrazekiella Brehm, 1949	X (13)	X (8)					
S.G. Ryloviella Borutsky, 1931	X (1)	X (2)					
S.G. Attheyella Chappuis, 1928	X (6)	X (2)	X (1)				
S.G. Canthosella Chappuis, 1931				X (4)			
S.G. Chappuisiella Brehm, 1926	?			X (3)	X (7)	X (6)	
S.G. Delachauxiella Brehm, 1926					X (20)	X (6)	
Echinocamptus Chappuis, 1928	X (3)		X (10)				
Maraenobiotus Mrázek, 1893	X (7)	X (2)	X (3)	X (2)	X (4)		
Afrocamptus Chappuis, 1932			X (1)				
Thermomesochra Itô & Burton, 1980				X (1)			
Elaphoidella Chappuis, 1928	X (22)	X (3)	X (17)	X (17)	X (8)	X (3)	
Epactophanes Mrázek, 1893	X (1)	X (1)	X (1)	X (1)	X (1)	X (1)	X (1)
Antarctobiotus Chappuis, 1930					X (4)	X (10)	X (2)
Loefflerella Rouch, 1962					X (4)	X (1)	
Antipodiella Brehm, 1928						X (3)	

PAL	PALAEARCTIC - Temperate Eurasia, Northern Africa, north of the Atlas Mountains	HOLARCTIC
NEA	NEARCTIC - North America to Central Mexico and Greenland	
ETH	ETHIOPEAN - Africa, Southern Arabia, Madagascar	PALAEOTROPICAL
ORI	ORIENTAL - Tropical Asia, Indo-Malay Islands	
NEO	NEOTROPICAL - Central and South America, South Mexico	
AUS	AUSTRALIAN - Australia, New Zealand, New Guinea and nearby Pacific Islands	
ARCH	ARCHINOTIC - Predominantly Antarctic	

The Neotropical contains many species of the genus Attheyella (subgenera Chappuisella, shared with the Oriental and Australian regions and Delachauxiella, in common with the Australian region), and the southern genus Antarctobiotus. Other genera present include Elaphoidella, where the two widely distributed species, E. bidens (Schmeil) and E. grandidieri (Guerne and Richards), are present together with several other endemic species, Epactophanes and Loefflerella.

The lack of much published data from Australia and many Pacific islands hampers discussion on the Australian region so that much of the information is based on work from New Zealand. From Australia is recorded Attheyella (Chappuisella and Delachauxiella), and species of Antarctobiotus. These are dominant members of the fauna in New Zealand. Elaphoidella is poorly represented in New Zealand, but present. The neotropical Loefflerella is also found in this country. Genera apparently endemic to New Zealand are Antipodiella and a new genus with Moraria-like features (Lewis, in prep.). Another new genus yet to be described, from terrestrial habitats, is common to both New Zealand and Australia.

The almost complete lack of early fossil records within the Copepoda prevents any accurate estimate of the age of harpacticoids or of the time when members ventured into freshwaters. Branchiuran type crustaceans are recorded from the Carboniferous (Hopwood, 1925). Euthycarcinus in Triassic deposits has often been cited as a copepod ancestor although present-day feeling is that this animal is not a copepod predecessor (Grygier, 1983). We assume that Copepoda already existed in the early Mesozoic. Palmer (1969) commented that all known fossil copepods were free-living harpacticoids and cyclopoids. He reports fossil copepods, including the harpacticoid Cletocamptus, from North and South America in lake deposits associated with boron minerals (Palmer, 1960), these from Miocene and Pleistocene periods. Sewell (1956) believed that the move from marine to freshwaters occurred at least in the Triassic, perhaps earlier. He considered that the three great families of freshwater copepods - the Diaptomidae of the Calanoida, the Cyclopidae of the Cyclopoida and the Canthocamptidae of the Harpacticoida - were probably all in existence in the Triassic or Jurassic when there was great contiguity of land masses encouraging an ease of dispersal. The opinion would seem to be that migration into freshwater reached its maximum in the middle of the Tertiary.

What then can we learn from present day distributions? Firstly we should perhaps look at the ease of distribution and dispersal of different species. It is significant that probably only two species appear to be true cosmopolits - Epactophanes richardi Mrázek and Elaphoidella bidens - and both of these species have the ability to reproduce parthenogenetically. Epactophanes, a monotypic genus, is found throughout the world. It is an extremely adaptable animal, showing great resistance, and found in many habitat types. Parthenogenetic reproduction often occurs within the species (Lang, 1935) although bisexual populations are common.

Although the genus Elaphoidella is found world-wide, only two species, E. bidens and E. grandidieri, are widespread. The former may be said to be a true cosmopolit, the latter is found throughout tropical regions (North and South America, Africa, Madagascar, Ceylon, Malaysia, Indo-China, Java, China, New Guinea and Hawaii). Typically along with this wide-ranging distribution is the occurrence of parthenogenetic reproduction and males are not known for these two species (Roy, 1931).

As we all well know, bisexual reproduction is the rule in Copepoda. Apart from these three species already mentioned, parthenogenesis has been shown to occur in a population of Canthocamptus staphylinus (Sarvala, 1979) and, on the basis of scarcity of males, is suspected in Elaphoidella leruthi Chappuis and E. elaphoides (Chappuis) in the northernmost part of their range (Chappuis, 1955).

Certain genera and species are known to produce resting stages, during which time they perhaps present the opportunity for increasing their range although, in reality, only those produced as drought-resistance stages have much dispersive opportunity. Summer encystment within adults is reported for Canthocamptus staphylinus (widely distributed in the Palaearctic), Attheyella wulmeri and A. northumbrica (Roy, 1932). In the case of C. staphylinus Sarvala (1979) suggests that although encystment may have evolved as a means of surviving in temporary pools which dry up in summer, for those species inhabiting the more permanent bodies of water it has remained advantageous, as a means of avoiding the period of most intense predation. The production of resting eggs is common amongst Bryocamptus (Arcticocamptus) species. The habitat type of several of the semi-terrestrial species presumably requires resistant stages of some description to enable them to survive desiccation but, like Frey (1980), I do not see these species being widely distributed by the usually postulated long-distance mechanisms of wind and migratory waterfowl. Damp, terrestrial bryophytic or litter-dwelling animals are usaully found amongst dense forest vegetation and bird migrants would have to be of the passerine variety. In this particular habitat, resistant stages, whatever they may be, function more in population survival than in facilitating dispersal.

So then, freshwater harpacticoids are animals which, in the main, are limited in their habitat type, sensitive to environmental changes and thus do not readily lend themselves to rapid active migration and extension of range. Apart from the ubiquitous Epactophanes and E. bidens, it is obvious from the table that most genera, are at least subgenera, within the Canthocamptidae, show a definite restriction of area.

It is generally assumed that the Palaearctic is the site of origin of the family, more precisely ancient Angaraland, the site of modern Eastern Asia (Borutsky, 1952). The most plesiomorphic genera are Canthocamptus, Bryocamptus, Attheyella (subgenera Mrazekiella, Ryloviella and Attheyella s. str.) and possibly Moraria, all of which are present here and all of which, incidentally, are present in the ancient Lake Baikal.

The large block of genera common to both Palaearctic and Nearctic shows the close faunal link between these two large continents. As previously mentioned, the Palaearctic is the richer and, in terms of genera, the Nearctic reflects an impoverished Palaearctic. Some of the most plesiomorphic species are found in the circum-polar regions of both continents confirming the original link between eastern Asia and North America. The genus Canthocamptus has five endemic species in Lake Baikal and, as the plesiomorphic C. staphylinus (Jurine), is widely distributed in North America. There are also common, or closely related species amongst the primitive Bryocamptus and Moraria. The close correlation of species and genera indicates a faunal interchange over some period of time. In terms of geological history, Bering Strait was formed quite recently and as late as the post Pliocene there was a link between northwest America and northeast Asia.

Canthocamptus then is a genus of the Holarctic, with species present in Europe, Japan, North America and North Africa (Fig. 1). The animals are large, inhabit various types of water body and exhibit cold stenothermy, passing the summer in an encysted state. In spite of their obviously ancient origin their geographical range is limited, due, no doubt, to their cold water stenothermy.

Bryocamptus is another genus of Eurasia and North America and its overall distribution is very similar to that of Canthocamptus (Fig. 1). However, some ecological distinctions can be made between the various subgenera. Members of the subgenus Bryocamptus s. str. inhabit mainly lowland regions in both main continents, Arcticocamptus is typical of the Arctic zone and alpine waters where members usually produce resting eggs which require water of low salt content and high acidity to hatch, while Limocamptus species occupy a variety of habitats including subterranean waters. A few species of Bryocamptus have been recorded from outside the Holarctic, particularly from the Oriental region, e. g. B. (B) zschokkei (Schmeil) and B. (L.) horai (Chappuis) are both reported from India. The finding of the genus in New Zealand (Harding, 1958; Lewis in prep.) is something of an enigma. A species seemingly identical with B. pygmaeus (Sars) is present in the South Island. Can we look to chance dispersal of this species which is ancient, well established throughout the Holarctic, polycyclic, eurythermal and can hibernate in an encysted form ? A further Bryocamptus species is found in forest litter in that country.

The distribution of Moraria is fairly similar to that of Bryocamptus with many surface-dwelling species in the Palaearctic and a few closely-related species in the Nearctic. Species showing reductive traits are numerous in subterranean habitats of western Europe.

The genus Paracamptus is represented by three species from Europe, one from Japan and two from

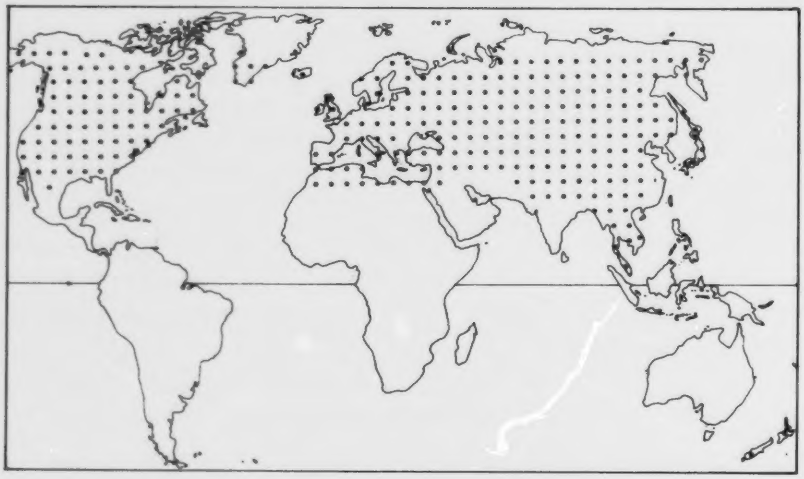

Figure 1. *World Distribution of Canthocamptus and Bryocamptus.*

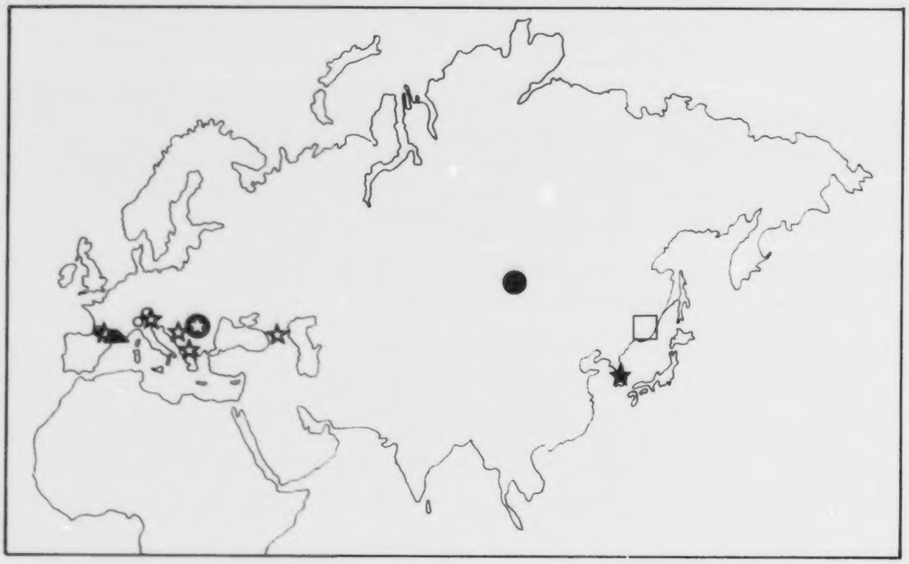

Figure 2. *Distribution of the endemic Palaearctic genera.*

☆ Ceuthonectes
○ Hypocamptus
★ Gulcamptus
✪ Spelaeocamptus
● Morariopsis
▲ Antrocamptus
□ Epactophanoides

Alaska.

Of those genera confined to the Palaearctic, (Fig. 2), Ceuthonectes is a Mediterranean inhabitant of subterranean waters which Borutsky believes is probably a relict of a more ancient fauna, Spelaeocamptus is probably derived from Elaphoidella and has two underground species in Roumania and Yugoslavia, Antrocamptus shows a very restricted range with nine species from caves in the Pyrenees, Hypocamptus, a genus closely related to Bryocamptus, has two species showing a preference for cold-water bodies of higher altitudes of The Alps and the Pyrenees, Morariopsis, presumably derived from Moraria, has two species endemic to Lake Baikal, Epactophanoides is described from subterranean waters of the Olga district in Russia and Gulcamptus is a subterranean species from South Korea.

The ancient genus Attheyella has a world-wide distribution with subgenera, however, restricted to distinct areas (Fig. 3). An eastern Asian origin has been suggested for this genus (Borutsky, 1952). Its apparent absence from central and southern Africa would suggest that the Gondwana-based subgenera Chappuisiella and Delachauxiella, had not moved into this continent before its early separation from the southern land mass in the early Cretaceous. The two solely Holarctic subgenera, Mrazekiella and Ryloviella, are most primitive in structure with Mrazekiella showing the most plesiomorphy. The subgenus is found mainly in eastern Asia. Ryloviella has one species in Lake Baikal and two in North America. Attheyella s. str. is a little more apomorphic in its features, approaching the Oriental Canthosella. It is found equally in eastern and western Europe with species also known from North America and in Africa. The closely related Canthosella has a tropical existence with species present in Sumatra, Java, Borneo and Vietnam. Delachauxiella and Chappuisella are dominant elements of the Neotropical and Australian fauna. Several species of Chappuisiella also inhabit Sumatra and Java. A single record from Germany, (A. (C.) aliena Noodt, 1956), is from tropical glasshouses and is more likely to belong to the country of origin of the plant or plants concerned.

Elaphoidella is a genus obviously closely related to Attheyella. As previously mentioned, it is found throughout the world but, apart from a few widespread species, particular regions have their own endemic fauna. Although many species are present in the Palaearctic, their distribution is strongly biased to the west and most of the species are exclusive to underground waters. For this particular genus a tropical origin is indicated. In the tropical countries all the Elaphoidella species are found in surface waters. It is believed that ancestors of the genus probably penetrated the Palaearctic in the Miocene, the tropical immigrants entering Europe, initially inhabiting surface waters as they do at present in tropical latitudes. Subsequent Pliocene cooling causes these forms to migrate to the warmer underground waters where they have persisted.

A fairly similar situation has arisen within a group of small cyclopoid copepods, all highly evolved, living in both subterranean habitats and amongst damp moss on the surface. In this case, however, we are dealing with several closely related genera rather than a single genus of many species. Prior to the discovery of four new genera from Madagascar (Kiefer, 1954), the discussion revolved around the four genera: Graeteriella Brehm, 1926, which is found throughout Europe in subterranean waters, moss and damp soil, Speocyclops Kiefer, 1937, also European but restricted to subterranean habitats, Bryocyclops Kiefer, 1927, represented in Asia and tropical Africa where all except one species live in surface microhabitats and Muscocyclops Kiefer, 1937, from South America, a moss and bromeliad water inhabitant. Chappuis (1927, 1933) believed that these animals were moss inhabitants in the Tertiary, when a tropical climate ruled in Europe and in the Quaternary they emigrated from the mosses to the subterranean waters. Lindberg (1954) discusses the origins of these several genera.

The genus Echinocamptus offers a closely parallelled situation. With approximately ten species in

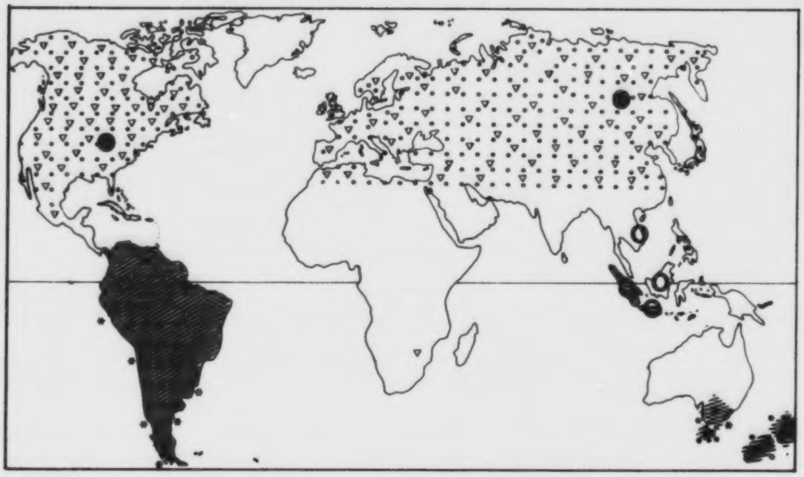

Figure 3. *Distribution of the subgenera of* *Attheyella.*

: Mrazekiella ● Ryloviella ▿ Attheyella s.str.

○ Canthosella ▨ Chappuisiella : Delachauxiella

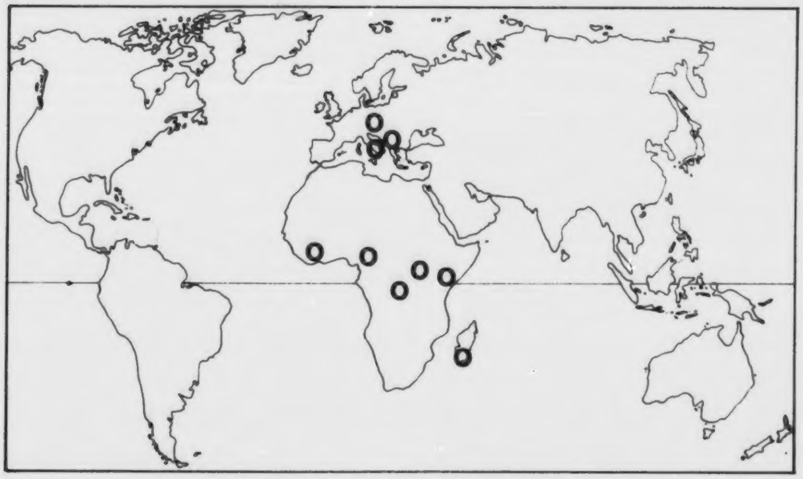

Figure 4. *World Distribution of the genus* *Echinocamptus.*

moss and ponds of tropical Africa (Ivory Coast, Cameroun, Kenya), two subterranean in Europe and a single moss inhabitant from Madagascar (Fig. 4), Chappuis (1956) assumes an African origin, probably derived from Attheyella, which emigrated into Europe and sought refuge underground when the climate became unfavourable.

Maraenobiotus is a widespread genus which is only absent from the Australian and Antarctic regions. This distribution indicated an ancient origin but the genus shows evidence of cold-water stenothermy, being restricted to high altitude bodies of water in the more tropical climates. It is reported from moist mosses in alpine brooks, the tundra zone and, infrequently, cold, lowland springs. Countries inhabited include western Europe, central and east Asia, Africa, North and South America and Malaysia.

The two genera appear to be Palaeotropical endemics. Afrocamptus is Ethiopean and restricted to French West Africa. It is closely related to Echinocamptus which is the dominant genus of this region. Itô and Burton's (1980) Thermomesochra seems not to be closely related to any true freshwater genera. In its possession of a degenerate antennal exopodite and mandibular palp, it is considered by these authors to be closest to the genus Pholetiscus Humes, 1947, one whose species are commensal with land crabs. A slight resemblance to certain Mesochra species is also shown by this strange thermophile.

We now move on to those genera with distinct southern origins and distribution. At present the list appears limited but there has been very little published work on the vast Australian continent and further South American investigations have yet to appear in press. Recent work in New Zealand has revealed at least three new genera (Lewis, in prep.), at least one of which is shared with Australia. A review of the New Zealand fauna appears in Lewis (1984).

The genus Antarctobiotus is recorded from the subantarctic islands of South Georgia and Possession Islands, South America, Australia and New Zealand (Fig. 5). this distribution must, in some way or another, use the former Antarctic land bridge between these continents. New Zealand lost its connections with Australia and Antarctica at about 80 M years BP whereas Australia remained connected to South America via Antarctica until 55 M years BP. There is much substantiating evidence from many other animal groups, particularly amongst the aquatic Insecta, that the formerly ice-free Antarctic has played an important biogeographic role in the distribution of the fauna (Brundin, 1966, 1967, 1970; Edmunds, 1972; Craig, 1969; Dumbleton, 1972; Ross, 1967, and Cowley, 1978).

There appear to be few morphological differences between the species of Antarctobiotus from the different countries except that all but one of the New Zealand species have only two setae on the antennal exopodite compared with three in all the others. Whether Antarctobiotus originated at some point in the Antarctic and moved both east and west, or whether it originated in the southern Neotropical region of South America, reaching New Zealand and Australia via the Antarctic bridge is open to speculation. By either passage, the long period of isolation of New Zealand would permit the slight divergence of the form of the antenna and the high degree of speciation.

This typical pattern of southern distribution is also shown by certain members of the calanoid family Centropagidae. Back in 1936, Brehm, in his study of the circum-antarctic distribution of the freshwater fauna, commented on the interesting distribution of the calanoid family "Boeckellidae" (= Centropagidae), especially of the genera Boeckella and Pseudoboeckella, Brehm divided Boeckella into two groups - a western one from Peru and Bolivia, through Chile, Brazil, Patagonia, the Falkland Islands and South Georgia. The eastern group occurs in Tasmania, the Australian mainland and New Zealand, with a single species occurring in Mongolia. He suggested that the genus had migrated southwards, dropping off the Mongolian and Peru-Bolivian species on the way. Marsh (1924), on the contrary, felt that the genus originated in the Antarctic continent and that the various species evolved from here, a view agreed to by Fairbridge (1945) who thought that the close relationship between the species in Western Australia and Mongolia pointed to a northern migration. Bayly (1979) has since synonymised the Mongolian species with the Australasian B. triarticulata (Thomson).

Brehm noticed that the close connections between Australia and New Zealand also extended to the other centropagid genera Gladioferens and Calamoecia, the former restricted to Australia and New Zealand, the latter to these two countries and New Guinea.

Bayly and Morton (1978) refer to the appearance of Boeckella in Mongolia (and Manchurai), pointing out that the revised view of Crawford (1974) on the present distribution of former parts of Gondwanaland helps to explain this, and similar distributions. Crawford believes that Tibet, the Tarim Basin and portions of northern China were formerly part of Gondwanaland. The cladoceran Daphniopsis is another with distribution patterns similar to Boeckella, which can be better understood in the light of this revision.

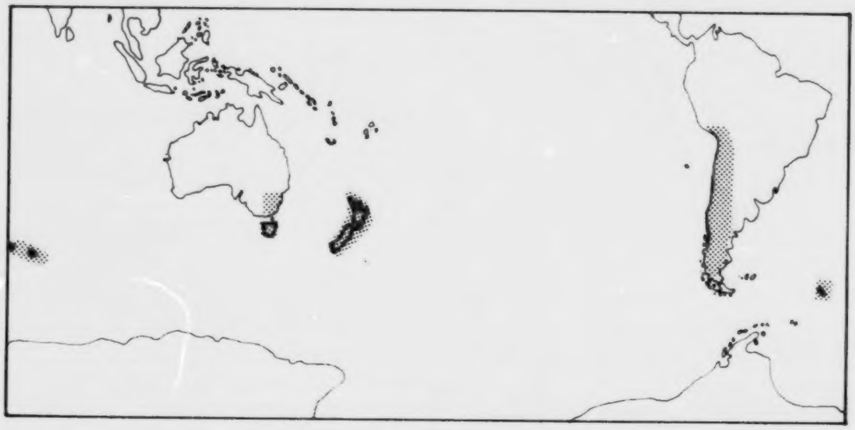

Figure 5. *Distribution of the genus Antarctobiotus.*

Loefflerella, with its rather meagre records of one species from Patagonia, three from Chile and one (as yet unpublished) from New Zealand permits little to be said of its presumably southern origins. It is a genus of the damp forest, having been found in terrestrial moss and forest-floor litter. Its distribution can be compared (if one can be permitted to use a crustacean example other than a copepod !) with that of the semi-terrestrial cladoceran, Bryospilus, which has representatives in Puerto Rico, Venezuela and New Zealand (Frey, 1980). Says Frey of the semi-terrestrial rainforest environment where both these genera occur: "Sufficient continuity of the wet forest habitat over long periods of time could make this habitat analogous to the ancient lakes of the world, and, under these circumstances, the fauna would be expected to have endemic, or uniquely adapted species."

The relationship of a genus between New Zealand and South America alone is one which is hard to explain when one considers the separation of the Southern land masses. Theoretically, there should either be a connection between Australia and New Zealand, Australia and South America or between all three. Any connection between New Zealand and South America alone can only be explained if there are allied species in Australia yet to be discovered, that habitat conditions here were never suitable or that the fauna, once established in Australia has succumbed to either overpowering competition or later unsuitability of habitat type.

The only described endemic Australasian genus is the New Zealand Antipodiella, synonymised by Lang (1948) with Epactophanes but which is, indeed, a distinct genus in its own right, with several species. Several other genera, unique to New Zealand and shared between that country and Australia have yet to be described while we eagerly await the results of current research on the fauna of Australia.

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BIOGEOGRAPHY OF BENTHIC HARPACTICOID COPEPODS OF THE MARINE LITTORAL AND CONTINENTAL SHELF

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In this recent review of crustacean biogeography, Abele (1982) made these comments about marine benthic harpacticoids:

1. Species tend to be widely distributed, even cosmopolitan.
2. Greatest diversity occurs in the tropics.
3. The majority of cosmopolitan species are associated with littoral algae.

His general conclusion is also relevant:

4. "distribution patterns of crustaceans appear to be best explained by a vicariance hypothesis under which previously wide-spread faunas have been modified by continental drift, opening and closing seaways, speciation, and extinction. This is not a testable conclusion but it appears to be consistent with the available facts" (Abele, 1982:290).

Abele emphasized that these conclusions must be treated with caution and regarded as tentative since a proper and rigorous analysis is inhibited by the lack of information on systematic relationships, fossil record, and present day distribution. These caveats about the Crustacea apply with particular force of marine benthic harpacticoid copepods.

Because of the vast size of his topic it is unreasonable to expect Abele's review to be comprehensive, or to be even in its treatment of the several crustacean groups, but it is unfortunate that the data he considered for harpacticoids either is rather old or is restricted in scope. The aim of this paper is to present a short review of modern data, and then to see if Abele's conclusions still hold.

Abele based his comments on the rather limited review by Sewell (1940) and the regional analyses of Wells (1967) for Inhaca Island, Mozambique and of Coull and Herman (1970) for Bermuda. Lang (1948) gives a much more comprehensive review than does Sewell, although he also only deals with species described prior to 1940-41. Lang refers to Sewell's paper only in an addendum.

Lang analyses his data according to the familiar marine zoogeographical regions proposed by Ekman (1935), which are based on macrofauna and which generally correlate well with oceanic surface current systems. In classical Darwin-Wallace dispersalist biogeographical theory this correlation is explained by the extensive dispersal powers of planktonic stages in the life cycle, but it can be debated whether this concept has much meaning for benthic harpacticoids (and most other meiobenthos). As far as is known, all benthic harpacticoids spend their entire life cycle in, on, or close to their preferred substratum, be it algae or sea grass (the phytal fauna) or sediment (the epibenthic and interstitial faunas; see Hicks and Coull, 1983, for definitions and examples of these faunal elements). They have been taken in surface waters only over shallow depths and close inshore (though it must be admitted that very little is known of the distribution of the nauplius larvae).

Thus, trans-oceanic dispersal via surface currents seems unlikely as a universal explanation for widespread distribution. Nevertheless, phytal harpacticoids have been found on floating Sargassum far from shore (e. g. Yeatman 1962). Similar pelagic transport mechanisms are at least theoretically possible (Gerlach 1977) and could explain some of the examples of disjunct distribution. Since the Sargassum fauna is species-poor and comprises eurytopic species of cosmopolitan distribution, and since littoral algae rarely remain intact and at the surface for long after becoming detached, it is doubtful if rafting by drifting algae, coconuts, logs, etc., can explain more than a small number of cases of amphioceanic distribution (Hicks 1977). However, such rafting is entirely plausible as a dispersal mechanism over small bodies of water and for short distances alongshore. This is true also for the influence of local current systems on dispersal.

Modern research (see Hicks and Coull, 1983, for a review) has refuted the traditional view that benthic harpacticoids are sedentary and confined to an association with the substratum so intimate that removal into the water column is distinctly disadvantageous. It is now known that many epibenthic and phytal, though not interstitial, species are found in the water column as a regular phenomenon induced by a variety of environmental cues (S.S. Bell and G.R.F. Hicks, pers. comm.). As such they are available to be dispersed by bottom currents; that this occurs is shown by the many experiments on recolonization of denuded sediments. Thus, the potential exists for extensive alongshore colonization and given the often very short time, days or even hours, taken to re-establish populations in denuded sediments, its magnitude and zoogeographic significance are probably much greater than previously believed.

Having rejected rafting, aerial dispersal via birds, and the influence of man as significant agents of trans-oceanic dispersal (see Gerlach, 1977, for a discussion of their potential), we are left with alongshore migration along the continental edge and continental drift as the only possible explanations for the majority of widespread distributions, both disjunct and continuous. That is, we are back to an agreement with Abele's general comment on crustacean distribution quoted at the beginning of this paper. Let us return to an analysis of distribution before commenting further.

Modern harpacticoid taxonomy is built on the foundations laid down by Lang (1948). His comprehensive revision recognized 1,208 species, 299 genera and 32 families in the Order Harpacticoida. Subsequent research based on Lang's scheme has raised these figures to about 3,000 species, 375 genera and 34 families.

Within this total Lang (1948) had to deal with a benthic marine littoral and shelf fauna of 892 species distributed among 181 genera (average 4.9 species/genus) in 24 families. Of these, 622 species were confined to one or other of Ekman's Regions, that is, 70 % of species were endemic in this broad sense. Closer analysis reveals that only a very few of these endemic species were not, in fact, confined within much smaller limits, e. g. Indian Ocean; east coast of North America; southern Australia-New Zealand. The overall pattern that emerges from Lang's analysis is a high degree of endemism coupled with a considerable level of disjunct distribution and a tendency towards widespread distribution, even true cosmopolitanism.

Lang's conclusions contrast with those drawn by Abele (1982:269) in the numerical emphasis given to endemism in the former and to widespread distribution in the latter. These differences arise from the nature of the analysis used. Lang looked at how the species are distributed throughout the world and discovered that 70 % have restricted distributions and 30 % wide distributions. In contrast, Abele's sources were primarily concerned with the limits of distribution of the fauna of a particular restricted locality. Thus, Wells (1967) found that 80 % of the species at Inhaca Island, Mozambique were of widespread distribution and less than 20 % endemic. These proportions, almost the opposite of Lang's, simply illustrate that the distribution of littoral and shelf benthic harpacticoid species tends to be either very local or very wide, with few intermediates. This conclusion is corroborated by analysis of the much more extensive data now available.

At the present time there are about 2,035 species of harpacticoids in the benthic fauna of the littoral and continental shelves (see Lang 1948, Bodin 1979, Wells 1976, 1978, 1979, 1981, 1983 for bibliography). They are contained in 304 genera (average 6.7 species/genus) and 25 families. This represents an increase on Lang's (1948) database of 128 % in species and 68 % in genera. This large increase reflects that since 1940 there has been both a steep rise in the quantity of research (and researchers) and the extension of studies to regions and habitats previously not well known. For example, the past 40 years has seen a great increase in data from the interstitial fauna of littoral sands and much more detailed investigation of shallow offshore sediments. This expansion of effort has also brought additional distribution records of older species, which have removed some of the disjunctions and increased the degree of cosmopolitanism for some species. For example, Robertsonia propinqua was known to Lang (1948) only from Bermuda, Gulf of Guinea and Bay of Bengal. Since then it has been found in the English Channel, Mediterranean Sea, Suez Canal, Maldive Islands, Mozambique, South Australia, New Zealand, Puget Sound and Argentina. Similarly, in Lang's analysis 269 species (30 % of the total) were restricted to the European boreal area; now that number is only 170, and represents only 8.4 % of the total. On the other hand, a large number of species, and some monotypic genera, of extremely local distribution has been added to the world fauna.

Through these additional data we now have an improved, though still not adequate, knowledge of the fauna of the South American Atlantic coast, East Africa, Bay of Bengal, New Zealand, Japan, Galapagos Islands, California, and at least a smattering of records from the west Pacific. This still leaves huge gaps, particularly with regard to the Indo-Malay region, the islands of the Pacific rim and the Pacific Plate, South American Pacific coast, Australia, and much of non-Mediterranean Africa. These gaps force judgements to be made about the limits of endemism and cosmopolitanism from very inadequate data. They also make difficult rigorous biogeographical analyses based on the methods of vicariance biogeography or panbiogeography such as have been possible and highly illuminating for some other marine groups (e. g. fishes - Rosen 1975, Springer 1982). In fact, such analyses are rendered essentially impossible through the dearth of detailed research on systematic relationships at either genus or family level; for example, no cladistic analysis of a harpacticoid taxon has ever been published.

Harpacticoid distribution must be analysed at the level of species. All families, except for Latiremidae with three species confined to the Mediterranean and one to Réunion Isle, and Neobradyidae with just the one species confined to north-west Europe, are widely distributed: most are cosmopolitan. This applies even to very small families. The Louriniidae, with one species, is pan-tropical; Parastenheliidae, with one genus and ten species, is cosmopolitan.

Most genera are widely distributed despite the often small number of species they contain (average 6.7; maximum species in a genus = 60; 90 genera are monotypic; only 27 genera contain 20 or more species). Zausopsis (Antarcto-Antiboreal), Parasunaristes (Indo-West Pacific), Karllangia (Indian

Ocean-Bay of Bengal) and Bradyellopsis (Mediterranean Sea) are the largest genera to be limited to what in Ekmanian terms would be a homogeneous area - each has just four species. 92 other genera are endemic, either to comparable homogeneous areas or more locally; 76 of these are monotypic, 14 have two species and 2 have three species. A good knowledge of the systematic relationships of these genera might provide real insight on harpacticoid zoogeography; unfortunately, such research has yet to be done. Thus, 204 genera (67 % of the total) are widespread, at least to the extent, that they are present either in two or more ocean basins or in two or more distinct latitudinal/water temperature belts.

For the present analysis the data have been partitioned among 89 localities based on the smallest areas described in Briggs's modification of Ekman's scheme (Briggs 1974, Ekman 1935, 1953). These localities have an integrity defined by the marine 'climate' on the one hand (mainly temperature and salinity) and non-pelagic dispersal possibilities on the other (mainly areas where only short stretches of open sea, usually shallow, separate an essentially continuous coastline). There are exceptions. In the Indo-Malay region and in the island chains of the Indian and Pacific Oceans there may be considerable stretches of deep water separating islands or island groups. These areas may eventually yield misleading data, but at this time the quantity they provide is so small that it is not a problem.

61.7 % of the world fauna (1,255 species) is endemic at the local level. Grouping these localities into larger areas does not materially alter this proportion. For example, 1,351 species (66.4 %) are limited to one or other of Briggs's (1974) Regions (e. g. Indo-West Pacific, Western Tropical Atlantic) and 1,389 species (68.3 %) to one of the five great latitudinal divisions adopted by Briggs (Northern Cold Temperate and Arctic; Northern Warm Temperate; Tropical Ocean; Southern Warm Temperate; Southern Cold Temperate and Antarctic). The small rise in proportion of endemic species with increasing area indicates that most of the non-endemic species have a rather wide distribution. In fact, 8,290 of species non-endemic at the local level (i. e. 640 species, 31 % of the total fauna) are present in at least two ocean basins or in two more distinct latitudinal/water temperature belts.

This conclusion from world data is supported by analysis at the local level. Analysis of localities where both phytal and sediment fauna are relatively well known (and these are very few) shows the proportion of endemic species in each local fauna to be low. In view of the low proportion of locally non-endemic species in the total world fauna, this must indicate that such species generally have a wide distribution.

localiy	**total species**	**endemic species**	**% endemic**
Laurentian	202	41	20.3
N. W. Europe	620	145	23.4
Mediterranean Sea	541	142	26.2
Black Sea	236	45	19.1
Bermuda	103	22	21.4
+Mozambique	128	38	29.7
+Red Sea	166	50	30.1
+Bay of Bengal	240	86	35.8

+ flanked by poorly known localities: therefore, proportion of endemic species may be unduly high.

What is the pattern of this cosmopolitanism? Just how are the species distributed? The following list sets out the confines of this large number of widespread species, here defined as species inhabiting at least two ocean basins or more than one latitudinal/water temperature belt.

distribution	**species**	
	No.	**%**
Truly cosmopolitan	54	8
Tethyan	70	11
Gondwanan	44	7
Arcto-Boreal	21	3
Arcto-North Atlantic	89	14
Arcto-North Pacific	4	1
Pan Northern Cold Temperate	12	2
Pan Warm Temperate-Tropical	27	4
Pan Atlantic	38	6
Pan Pacific	0	0
Indo-West Pacific	35	5
Trans-Panama	11	2
North Atlantic-Mediterranean	235	37

It is unlikely that these figures represent an accurate assessment. Dominated as they are by species distributed in the North Atlantic-Mediterranean region, they only reveal our comparative ignorance of the rest of the world's fauna. But they do suggest three conclusions:

1. True cosmopolitanism does exist. Although the list includes probable as well as certain cosmopolites, there are at least 36 species where little doubt can exist, including two that are known from many locations in all the ocean basins and at all latitudes.
2. The present distribution of some species can be explained by regarding them, or their immediate ancestors, as part of an indigenous Gondwana fauna. Since they all belong to widespread genera only an analysis of systematic relationships within these genera can determine the validity of this explanation.
3. Another significant number of species have distributions restricted to two or more of the modern remnants of the ancient Tethys Ocean (Mediterranean Sea, Bay of Bengal, Indo-Malay region). The same caveat applies to these as to the presumed Gondwana group.

Abele's second conclusion (1982:292) was that benthic harpacticoids have their greatest diversity in the tropics. The data do not directly support this but show instead that each of the Northern Temperate Regions have more species than the tropics. However, the difference is not great and bearing in mind that we have no data from large areas of tropical shores, and the very high proportion of endemic species in the tropics, it is most probable that diversity is much greater than presently indicated. It is also almost certain that the southern hemisphere is underrepresented by current data.

Abele (1982:269) quotes Sewell (1940) as the authority for his third comment, that the majority of cosmopolitan species are associated with littoral algae. Sewell's remark remains correct today, but its value is rather limited. Despite the fact that distinct phytal, epibenthic and interstitial habitats are readily recognized, relatively few species are clearly morphologically adapted to just one of them. Algae always host species that are equally common in the epibenthos of the surrounding mud, sand or gravel: and vice versa. Certainly, algae from exposed rocky substrata have a greater proportion of primarily phytal species, and an estuarine mud flat a greater proportion of primarily epibenthic species, but as the two habitats come closer together spatially the communities tend to merge. The greater knowledge of epibenthic communities gained in recent years has blunted the edge of Sewell's comment. Among the 54 species here considered cosmopolitan, only 17 are primarily phytal, though all 54 are regular inhabitants of algae and sea grasses.

Region	total species	endemic species	% endemic
1. Arctic	201	46	22.9
2. Northern Cold Temperate	836	327	39.1
3. 1. and 2. together	887	421	47.5
4. Northern Warm Temperate	860	345	40.1
5. Tropical Oceans	752	474	63.0
6. Southern Warm Temperate	180	71	39.4
7. Southern Cold Temperate	214	99	46.3
8. Antarctic	52	27	51.9
9. 7. and 8. together	244	111	45.5

Interstitial species, however, tend to show a higher degree of local endemism (76 %) than primarily epibenthic or phytal species (63 % and 68 % respectively). None are truly cosmopolitan, though a few do have a rather wide distribution.

The analysis so far, with its demonstration of a high degree of local endemism at the species level; a relatively large number of monotypic genera; many small genera, but with widely distributed species; the wide distribution of the vast majority of non-localised species; the cosmopolitanism of all families except for two very small ones; strongly suggests that benthic harpacticoids do conform to the vicariance model suggested by Abele (1982:290) for crustaceans as a whole. Also, since trans-oceanic dispersal via pelagic life stages, rafting, etc., seems an unlikely explanation, such a distribution must indicate an ancient fauna that has become widespread through tectonic processes and alongshore drift. Patterns of species endemism and restricted distribution are likely to be of more interest, therefore, than patterns of wider distribution. Unfortunately, the limitations of our data prohibit rational discussion.

Some comment is possible, however. Sewell (1956) gives convincing evidence of primary Gondwana distributions, with the opinion that these were achieved by dispersal along the Pacific margin of Gondwana and subsequent translation via continental drift. These examples range from species within cosmopolitan genera to whole genera. Recent data reinforces this opinion (Hicks 1977). Sewell's example of Onychocamptus chathamensis (Cape Town, Bombay, Calcutta, Sydney, Melbourne, Chatham Is.) is joined by its congener, O. bengalensis (Aldabra, Madras, Calcutta, Sydney). The distribution of Perissocope as now known extends Sewell's argument about this genus with possible evidence of speciation accompanying a northward extension of its range consequent on the opening of the Atlantic Ocean. Unfortunately, this hypothesis does not explain the presence of the endemic P. bayeri in the Caroline Islands.

Perissocope typicus	Antarctica
P. littoralis	Campbell Is.
P. exiguus	Patagonia
P. xenus	Angola, west Mediterranean
P. adiastaltus	Scilly Is.
P. cristatus	Lesser Sunda Is.
P. bayeri	Caroline Is.

The genus *Zausopsis* is clearly Godwanan in origin.

Zausopsis mirabilis	Patagonia,Tristan da Cunha, New Zealand, Campbell Is., South Georgia
Z. kerguelensis	Kerguelen
Z. contractus	New Zealand, Macquarie Is.
Z. luederitzi	Namibia

At the community level, Hicks (1977) demonstrates that the phytal fauna of central New Zealand has its strongest affinities with Patagonia and not with southern Australia, its nearest cold temperate neighbour to the west. Hicks argues strongly that it is plate tectonics, and not the West Wind Drift, that has played the major role in the present distribution of the fauna of southern hemisphere cold temperate regions.

The fauna of the eastern and western shores of the Atlantic Ocean should also provide evidence of the role of continental drift in harpacticoid dispersal, such as has been demonstrated for several groups of the non-copepod interstitial fauna (Sterrer 1973). But, again, we lack the systematic analysis that could reveal the presence of transoceanic sister species or monophyletic groups. There are a few pointers in this direction. The only two species of *Pararobertsonia*, *P. abyssi* and *P. chesapeakensis*, are endemic to Norway and Chesapeake Bay respectively. *Longipedia helgolandica* and *L. americana* are morphologically similar (Wells 1980) and both may be descended from *L. minor*, which is restricted to north west Europe and the Mediterranean Sea. *L. helgolandica* is not known in the Mediterranean but is present along the eastern Atlantic littoral from Europe to Namibia. *L. americana* occurs along the western Atlantic littoral from Massachusetts to Brazil and, perhaps interestingly, is also found as a distinct subspecies in the Galapagos Islands.

Arenosetella germanica is one of the few widely distributed interstitial species, occurring throughout the northern temperate and tropical regions. Significantly, while it is common in Atlantic Europe it is not present on the east coast of North America, where it is replaced by *A. spinicauda* which, morphologically, is a possible sister species. Is this an example of isolation, vicariant speciation, and extinction? Other probable examples of vicariance can be found.

Longipedia coronata, *L. kikuchii* and *L. nichollsi* from a morphologically discrete group in the genus (Wells 1980) that is distributed from Iceland through north west Europe to the Mediterranean and Red Seas (*L. coronata*); from the Bay of Bengal through the Indo-Malay region to southern Japan (*L. kikuchii*); and in South Australia and Fiji (*L. nichollsi*). The distribution of *L. coronata* and *L. kikuchii* could be interpreted as representing a Tethyan remnant, but the distribution of *L. nichollsi* makes it more probable that the ancestor of these species was pan warm temperate-tropical.

The genus *Tigriopus* occurs in three distinct geographic groups (Bradford 1967):

1. Atlantic	*Tigriopus brevicornis*	N.W. Europe: Madeira
	fulvus	Lusitania: Mediterranean
	minutus	Senegal
	brachydactylus	Angola
2. North Pacific	*japonicus*	Japan
	igai	Bonin Is.
	californicus	California: Washington State
3. Gondwanan	*angulatus*	Chile, Patagonia, Tasmania, southern New Zealand, Macquarie, Kerguelen, Antarctica
	raki	northern New Zealand

The morphological differences between these species are small and on present data it is unrealistic to say that the geographic groups are monophyletic, but the genus could represent vicariant speciation of a cosmopolitan ancestral population. Further, the distribution of at least the Atlantic species has a clinal quality about it.

A similar situation exists in the genus *Karllangia*, which has four species:

Karllangia tertia	East London
K. psammophila	Mozambique
K. arenicola	Red Sea
Karllangia sp.	Andaman Is.

In this case *K. tertia* probably is the most primitive species and thus the distribution on the east African shore could support a dispersalist theory based on a southern origin. Given this possible hypothesis, the close morphological similarity between the as yet undescribed Andaman Islands species and *K. psammophila* and *K. arenicola*, the two more derived African species, may be fortuitous and indicate its independent vicariant origin from a widespread *tertia*-like ancestor, perhaps also of Gondwanan affinities. I have no knowledge as yet of what might be the sister group of *Karllangia*.

Finally, there are several species with a Trans-Panamanian distribution. Similar distributions of monphyletic groups of species undoubtedly await detection.

	Pacific	**Caribbean/Atlantic**
Arenosetella panamensis	Panama	Panama
Noodtiella hoodensis	Panama Galapagos	Panama
Leptastacus jenneri	Panama	Panama North Carolina
Arenopontia gussoae	Panama	Cuba
Pseudobradya pulchera	California	Virgin Is.
Zausodes septimus	California	Virgin Is.
Harpacticus pulex	California	Florida
Amphiascus undosus	California Vancouver Is.	Florida
Schizopera knabeni	California Vancouver Is.	Louisiana South Carolina
Halectinosoma kunzi	California South Carolina	North Carolina
Scottopsyllus pararobertsoni	California	Bermuda

The distribution of those species common to Caribbean-Bermuda and Pacific Central America or the Galapagos Islands can be explained either by the classical dispersalist theory involving cross-migration at times of oceanic congruence across the Central American isthmus, or by the plate tectonic dependent theory put forward by Rosen (1975) for Caribbean fishes. This theory relies on the belief that the Caribbean Plate was formed by an intrusion from the then existing East Pacific Plate. The Caribbean benthic fauna thus is derived from Pacific ancestors, not Atlanitc ones. The problem concerns the species common to California and Caribbean-Bermuda. California was too far removed to have been concerned in the tectonic movements involved in Rosen's theory, and modern northern California, presently at least, is in a much cooler water temperature zone. These intriguing distribution patterns can only become more than a source of frustration when we know where the nearest relatives of these species are distributed and, of course, when we have much more data from tropical central America.

These few examples only serve to illustrate the depth of our ignorance and underline the obvious conclusion that a rational theory of the biogeography of marine benthic harpacticoid copepods is not yet possible.

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BIOGEOGRAPHY OF PARASITIC COPEPODS

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Abstract: Two closely related families of parasitic copepods are compared morphologically and biogeographically. The family Taeniacanthidae exhibits morphological features primitive to those of the Bomolochidae. The taeniacanthids are predominately Indo West Pacific-East Atlantic with less than 20 % of the currently valid species occuring in the Western Atlantic and East Pacific. The Bomolochidae, on the other hand, have nearly as many species represented in the Western Atlantic-East Pacific as in the Indo West Pacific-East Atlantic.

INTRODUCTION

In his excellent review of the "state of the art" of copepod parasites of fishes, Kabata (1981) has no reference to any biogeographical information about the group. In 1983, Ho commented on the biogeography of Japanese surfperches inferred from their copepod parasites. To the best of my knowledge this was the first use of marine parasitic copepods in a biogeographical analysis. The present paper appears to be the first attempt to analyze the biogeography of parasitic copepods using contemporary comprehensive works.

DISCUSSION

Although considerations of the biogeography of parasites must take into account environmental parameters such as temperature, media, wind, and other physical and biological factors, the singlemost important factor in parasitic copepod biogeography is the role of the host. Also, it is important to consider the modifications in parasite life cycles when compared with their free-living counterparts.

Parasites generally exhibit life cycle modifications designed to overcome the hazards of their parasitic way of life, especially the need to locate and establish themselves with their hosts. Modifications involve such strategies as: increased fecundity; multiplication of individuals while in immature stages; acceleration of molting cycle time; and reduction in the numbers of free-living stages.

Parasitic copepods utilize primarily the latter two methods. Although few life cycles for parasitic copepods have been worked out in the laboratory, those that have support this. As an example egg sacs of Kroyeria sp. that I put in sea water in the laboratory molted to their infective stage in less than 24 hours (unpublished). It can be reasonably assumed that parasitic copepods exist in the plankton for a considerably shorter period of time than their free-living counterparts, and that they attach to their hosts as quickly as possible. These life cycle modifications directly affect the biogeography of parasitic copepods and, most importantly, their dispersal capabilities. Consequently, rather than physical factors such as currents and winds, so important to the dispersal of free-living plankton dwellers, the host is

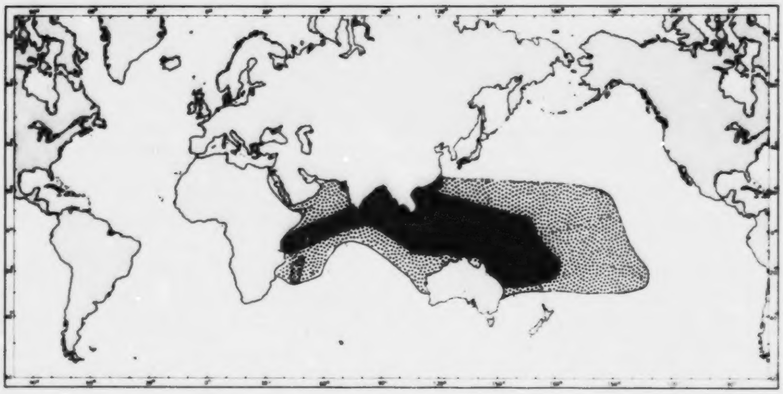

Figure 1. *Distributions of the host, Synodus variegatus (light stipple) and its parasite, Metataeniacanthus vulgaris (dark stipple).*

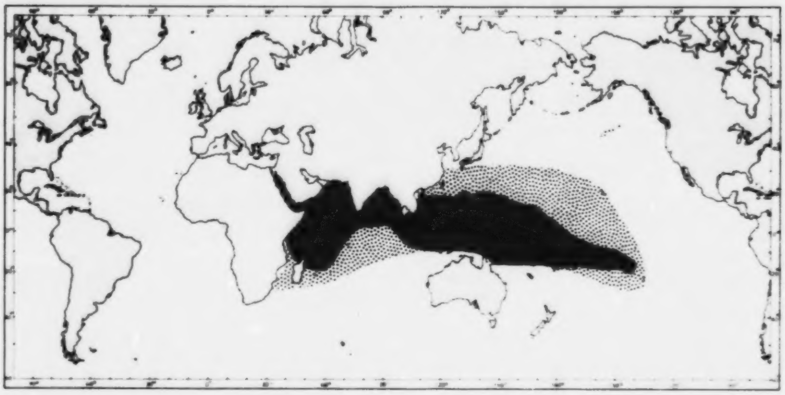

Figure 2. *Distributions of the host, Synodus englemani (light stipple) and its parasite Metataeniacanthus epigri (dark stipple).*

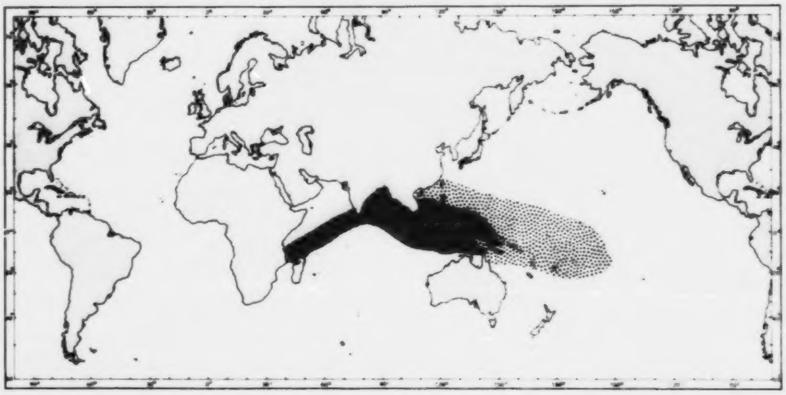

Figure 3. *Distributions of the host, Synodus jaculum (light stipple) and its parasite Metataeniacanthus conepigri (dark stipple).*

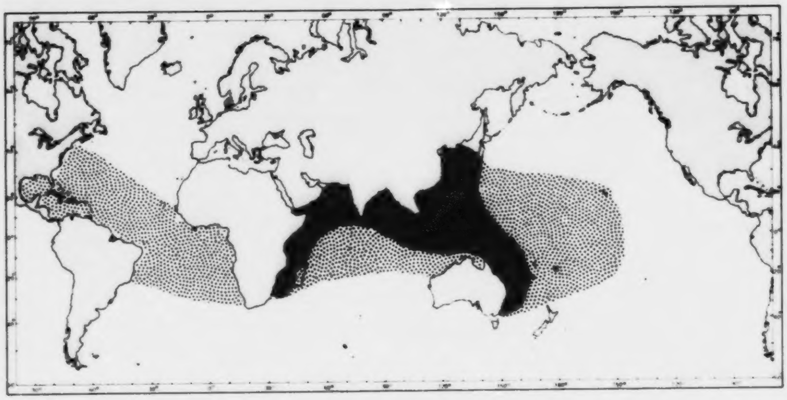

Figure 4. *Distributions of the host, Trachinocephalus myops (light stipple) and its parasite Metataeniacanthus synodi.*

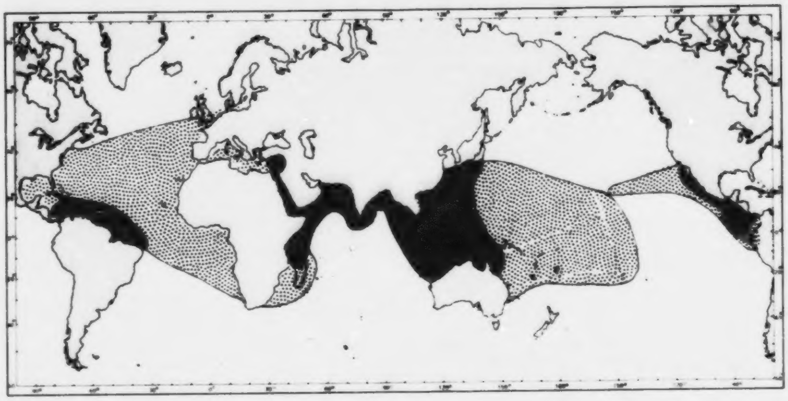

Figure 5. *Distributions of the host, Euthynnus alletteratus (Atlantic), E. affinus (Indo-West Pacific), and E. lineatus (E. Pacific) (light stipple) and their parasite, Unicolax collateralis (dark stipple).*

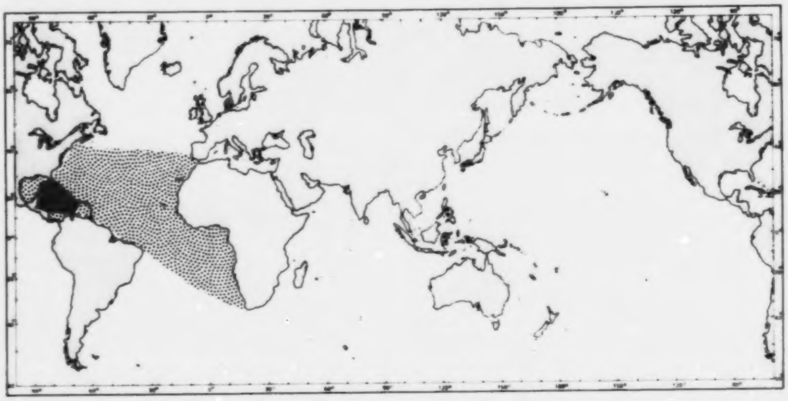

Figure 6. *Distribution of the parasite genera Ceratocolax (light stipple) and Acanthocolax (dark stipple).*

most important in the dispersal of parasitic copepods.

This discussion is based primarily on 4 comprehensive studies of copepod parasites of 3 widely distributed fish groups: Copepods and Needlefishes: a study in host-parasite relationships (Cressey and Collette, 1970); The parasitic copepods of Indo-West Pacific lizardfishes (Cressey and Cressey, 1979); Parasitic Copepods of Mackerel- and Tuna-like Fishes (Scombridae) of the World (Cressey and Cressey, 1980); and Copepods and Scombrid Fishes: a study in host parasite relationships (Cressey, Collette, and Russo, 1983).

After examining the distribution patterns of parasitic copepods and their fish hosts, 2 patterns of distribution emerged. The first pattern I would like to discuss is the relationship between the distribution of the host and that of its copepod parasite.

Figures 1-4 show the distributions of 4 species of Indo-West Pacific lizardfish (*Synodus variegatus*, *S. englemani*, *S. jaculum* and *Trachinocephalus myops*) and their taeniacanthid copepod parasites (*Metataeniacanthus vulgaris*, *M. epigri*, *M. conepigri* and *M. synodi*) which are specific to their respective hosts. The 3 species of *Synodus* are widely distributed throughout the Indo-West Pacific. The ranges of their parasitic copepods, however, are more restricted and, in general, central to the distribution of the host. The lizardfish *T. myops* is found in the Atlantic as well as Indo-West Pacific (Fig. 4). Its parasite (*M. synodi*) is found infesting only the Indo-West Pacific hosts.

If the hosts are the primary dispersal mechanism for the parasites, why are they not found throughout the host range? The answer probably lies in the life cycle modifications of the parasite and dispersal mechanism of the hosts. As pointed out earlier, parasitic copepods abbreviate their life cycles to a minimum number of free-living stages. In order for a parasite species to succeed, it must reestablish its parasitic mode of life as quickly as possible after it has been released into the plankton. Consequently, dispersal by currents, winds, etc., would be counterproductive factors, as they could carry the free-living stages away from the host territories. Studies of larval fish indicate that parasitic copepods rarely infest larval fish (G.D. Johnson, pers. comm.).

Rather, evidence indicates that reinfestation occurs on host fish after the host has reached a postlarval stage. Since the primary distribution of fishes is a result of distribution of larval fishes by currents and other physical factors, and since parasitic copepods are generally not found on larval fishes, the distribution of the parasite lags behind that of the host as indicated by the examples given in Figures 1-4.

Van der Spoel (1983) states that distribution of neritic species is west to east. Figures 1-4 show that, for the most part, the parasite is found in the westernmost portion of the host's range and absent from the easternmost portion. Figure 5 shows the disjunct distribution of the widely distributed parasite *Unicolax collateralis* on the 3 species of *Euthynnus*. This copepod is found on 4 other scombrid species as well. Does this distribution pattern indicate that the centers of origin or dispersal are in the areas of parasite infestation? Manter (1961) claimed that a host species had fewer species of parasites as it dispersed from its center of origin (or dispersal). This was demonstrated by Cressey, Collette and Russo (1983) in the case of *Scomberomorus commerson* which had 9 parasite species in the northern Australian area, 5 parasite species further north, 7 species further west in the Indian Ocean off India and East Africa, and only 3 species in the Red Sea.

The Pacific Plate may present a barrier to the distribution of neritic and distant neritic parasitic copepods, but in the five examples presented, one copepod species (*Metataeniacanthus epigri*, Fig. 2) is found on hosts on the Plate. Does this indicate that *Synodus englemani* and its parasitic copepod are the oldest of the extant species of both groups?

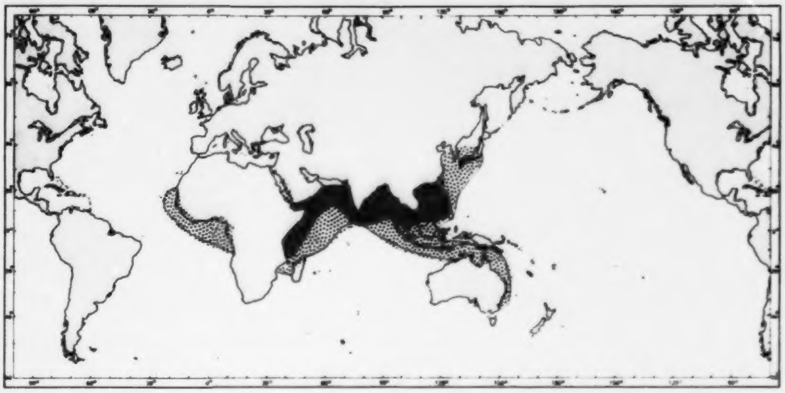

Figure 7. *Distributions of the parasite genera* *Pumiliopes* *(light stipple) and* *Pumiliopsis* *(dark stipple).*

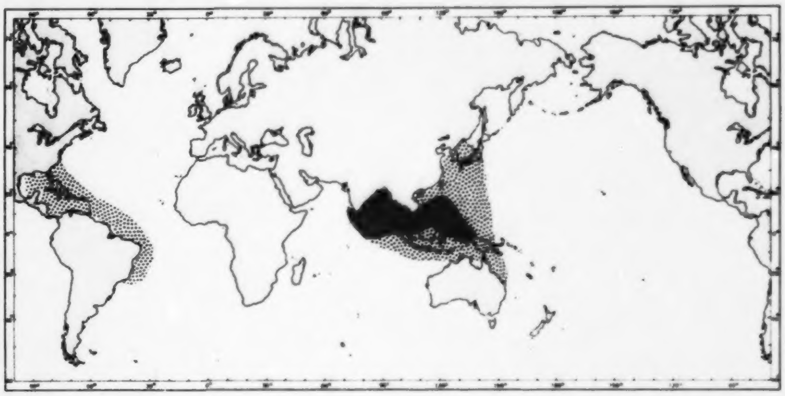

Figure 8. *Distributions of the parasite genera* *Orbitacolax* *(light stipple) and* *Pseudorbitacolax* *(dark stipple).*

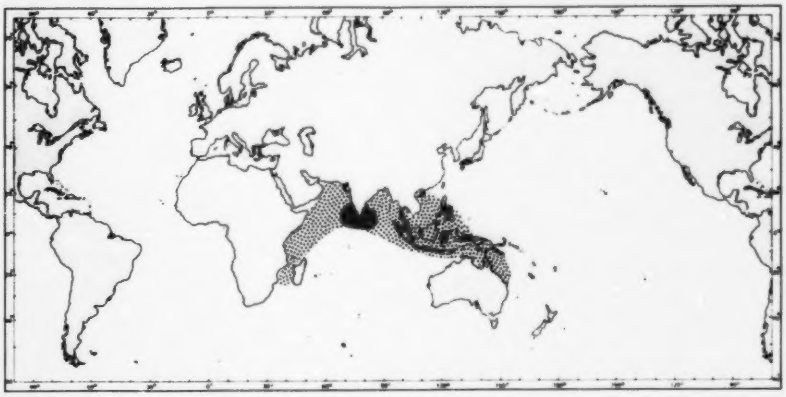

Figure 9: ***Distributions of 2 species of a new genus (light and dark stipple) closely related to the circumtropical genus*** ***Nothobomolochus*** ***(not plotted).***

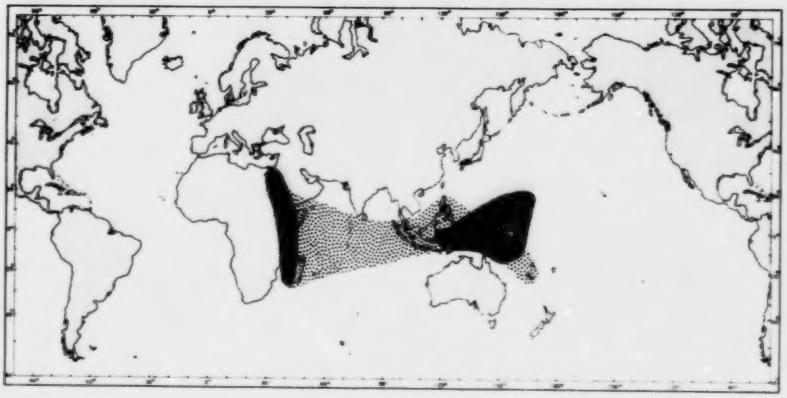

Figure 10. *Distributions of 3 genera of Indo-West Pacific taeniacanthid copepods parasitic on Indo-West Pacific echinoids;* *Echinirus* *(dark stipple, Africa coast),* *Clavisodalis* *(dark stipple, western Pacific), and* *Echinosocius* *(light stipple, Indo-West Pacific).*

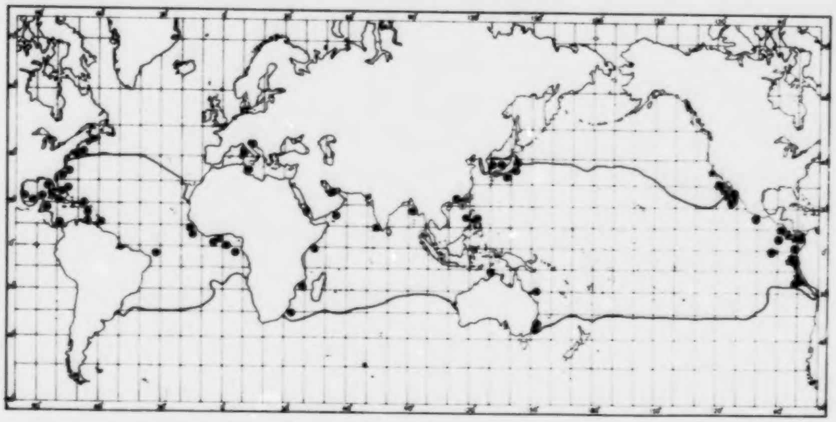

Figure 11. *Distributions of 3 closely related bomolochid copepods;* *Bomolochus* *bellones* *(dots), and* *B.* *sinensis* *(stars in circles, W. Pacific), and* *B.* *enciculus* *(stars, E. Pacific).*

The second pattern and subpatterns that emerge concern the biogeographical relationships between closely related parasite taxa. This pattern indicates that when the distributions of closely related parasite taxa on closely related hosts are compared, one parasite taxon is always more widely distributed than the other(s), and that they are always sympatric. Figures 6-11 illustrate examples of this.

Figures 6-9 show the distribution of 4 sets of related bomolochid genera, which occur in both the Atlantic and Indo-West Pacific. The distribution of Nothobomolochus is circumtropical and therefore not plotted on Figure 9. I am in the process of removing 2 species from the genus and designating a new genus to contain them. They are Nothobomolochus digitatus and N. denticulatus and are reported from beloniform fishes of the Indo-West Pacific. In each of the 4 examples there is one widely distributed species and one or 2 species with more restricted distribution(s) within the range of the first species.

Figures 9-12 in Cressey, Collette and Russo (1983) show the distributions of closely related species of Caligus parasitic on scombrid fishes (these figures are not repeated here). The distributions are similar, geographically, to those of the bomolochids. But the pattern is of a restricted species in or near the center of the range of a more widely distributed species.

Figure 10 indicates the same wide and restricted sympatric distributions. But the restricted species, rather than being central, are at the east-west margins of the widely distributed species. The copepods represented in Figure 11 are parasites on belonid fishes. Both the hosts and copepods from the eastern Pacific are endemic. Bomolochus sinensis, from the seas surrounding southeast Asia, is reported from Ablennes hians, a circumtropical species, and Strongylura strongylura, a species restricted to southeast Asia. The parasite B. bellones is circumtropical and reported from 16 species of belonid fishes. Figure 10 is based on data from Dojiri and Humes (1982). The 3 taenicanthid genera are parasites (associates?) of indo-West Pacific holothurians.

One further point relative to this discussion is that the principles of island biogeography may well be applicable to parasitic copepod biogeography. In a few cases of the parasites considered here I have attempted to apply some of these ideas. The results were inconclusive. One problem may be in defining "island" as it relates to hosts. Is it the species, the individual, the distribution, or a combination of these and other factors? Although this initial attempt to apply island biogeography to parasitic copepods was inconclusive, I still feel that this would be a fruitful pursuit.

The study of parasite biogeography is in its infancy and many ideas remain to be presented; some will be discarded, others, I hope, will begin to show some light at the end of the tunnel. I have no illusions that those presented here will withstand the test of time, but, if nothing else, may stimulate fruitful research.

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4. Behavioural Ecology (Chairman: *B.M. Marcotte*)

HERMENEUTICS AND COPEPOD BEHAVIOURAL ECOLOGY: SCIENCES OF INTERPRETATION

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> *"'I was sent only to the lost sheep of the House of Israel'. But the woman had come up and was kneeling at his feet. 'Lord,' she said, 'help me.' He replied, 'it is not fair to take the children's food and throw it to the house-dogs.' She retorted, 'Ah yes, sir; but even house-dogs can eat the scraps that fall from their master's table.'"*
>
> *Gospel by Matthew 15:25-27*

The sensory environment of copepods is not the world we experience. Benthic copepods locomote and forage slowly in a boundary layer of water near the bottom in which frictional forces result in an exponential decrease in water velocity with depth toward the sediment (Hinze, 1959; Neuman and Pierson, 1966; Wimbush, 1976). Water movements, universally governed by viscous and inertial forces, are here viscosity dominated. Non-turbulent or laminar movements of water results (Hinze, 1959; Neuman and Pierson, 1966; Wimbush, 1976). Chemicals produced or consumed by food organisms inhabiting this boundary layer diffuse slowly and the three-dimensional gradients thus produced move across the bottom along predictable trajectories. Benthic copepods forage using chemoreceptors on their first antennae (and sometimes on other oral appendages) to detect these chemical gradients to locate patches of food. Propreoreceptors are also used to feel food on surfaces and to permit the efficient handling of food bearing particles (Marcotte, 1977, 1983, 1984).

The path traversed by foraging benthic copepods seems at first randomly directed. Repeated observations, however, reveal that a copepod stops from time to time along its path and then proceeds and loops back and crosses its path usually at points where the animal had previously stopped. It is possible that when the animal stops it secretes a pheromone into the water or onto the sediment thus creating a transient coordinate system for mapping the habitat. This may help reduce the probability of the copepod repeating the same foraging path in a short time interval, the length of which is set by the pheromone's diffusion rate and the ambient water motion. Pheromones have also been invoked to explain copepod mating behaviour (Parker, 1901; Katona, 1973), the homing behaviour of intertidal copepods (Bozic, 1975) and the supression of development in field and culture populations (Smoll and Heip, 1974; Walker, 1979).

Benthic copepods display complex trophic behaviours, especially food selection, which are not easily categorized in conventional trophic-dynamics paradigms. They appear not to be strict "herbivores", "carnivores" or even "omnivores". They eat selectively but not exclusively. The geometric dimensionality of food bearing particles seems to be a prerequisite for feeding responses. Some copepods feed only on cylindrical algal filaments and rectilinear edges of grass, others sweep food from planar surfaces of grass, algae and/or sand and still others treat the world as fully three-dimensional - crushing prey, sorting food from among clay floccules and scraping food from the surface of spheres of flocculated debris (Marcotte, 1977, 1983, 1984). Some copepods eat diatoms by shearing open the frustrule and ingesting the cell sap. For these, and other copepods, analysis of gut contents may be an exercise in futility. Behavioural flexibility and great manual dexterity are rules among these taxa and are very little studied.

Harpacticoid copepods and other benthic taxa exhibit diel rhythms in their locomotory and feeding behaviours. Their activity levels peak crepuscularly. Many "inbenthic" harpacticoids can be found swimming above the bottom and presumably interacting with planktonic organisms (as predators, prey, competitors, etc.) during the night (although tidal rhythms, diel rhythms in the vertical distribution of phytoplankton and seasonal rhythms in copepod abundances on the bottom can modulate this diel periodicity) (Marcotte, 1984; Marcotte et al. submitted; Pers. obs.). Locomotory behaviours may also be modified by responses to and/or the selection pressures of predators. Visually foraging predators, such as Atlantic or Pacific Salmon juveniles, locate prey on the basis of differential prey motion against a kinematically active background and other characteristics. Tactile predators, such as some amphipods, locate prey on the basis of vibrations conducted through the water (Marcotte, 1983). Copepods respond to incoming tactile stimuli, e. g. bow wave of an approaching predator touch of a competitor, etc. by either running, "playing dead" or by frequenting habitats unsuitable to the principle sensory modality of the predator, e. g. dim, turbid waters among marsh grasses or in the nepheloid layer in deep water when visual predators are involved. (Other predator avoidance adaptations are also possible. Cf. Marcotte, 1983). Which strategy is appropriate to any given stimulus will depend on the dominant sensory modality and foraging strategy of the predator. Since the copepod only perceives a predator or competitor by the vibrations it produces, the meaning of the stimulus is ambiguous. The copepod may respond "incorrectly" to any given stimulus: playing dead when a tactile predator approaches, running when a visual predator approaches. Perception of the frequency of the incoming vibration by the copepod may help limit or resolve this ambiguity but probably can not eliminate it. Thus the response of a copepod to any one stimulus may appear stochastically variable yet the variance is not meaningless "noise" but evidence of an ambiguity in the animal's perceptual skills (Cf. Marcotte, 1983). This perceptual ambiguity, however, must not be confused with the systematic ambiguity engendered by representational and computational aspects of the animal's cognition (See Marcotte, 1983 for a fuller discussion of these distinctions and their natural selection implications).

To interpret scriptures written in the frist Century A. D., one must use dictionaries of that century and one must attempt to discern the layers of editorial and other revisions which occurred to the manuscripts between their first writing and their subsequent duplication, distribution and cannonization. In the context of this time and culture, Matthew portrays a thrice radical event in the life of the hero (sensu Campbell, 1968). A woman - female, gentile, foreigner - exercises enormous power over Jesus. She calls him to a more complete, inclusive wholesome understanding of his mission.

The behavioural ecology of copepods forces a thrice radical revision in evolutionary ecology: perspective, method and substance. The recognition that organisms interacting, predator-prey, competitors, etc., through sensory modalities which are non-congruent, renders fossil paradigms of natural selection based on external objective observers, i. e. non-solipsistic paradigms of optimal foraging, trophic dynamics, etc. (Marcotte, 1983). With this change in perspective, it becomes meaningful, indeed urgent, to ask, "Can an organism adapt to an unperceived selection pressure?" and "Can organisms do more with life threatening yet unperceived selection pressures than live where the pressures not existing or extinct?" The recognition that copepod behaviours have complex choreographies rich in meaning and perceptual and cognitive ambiguities renders fossil methods which attempt to classify copepods in *a priori* categories defined on gut contents, etc. Copepods do not occupy a preconceived (by a human) niche, they define it. Behaviourally defined resources are the currency of their evolutionary exchanges (Marcotte, 1984). Finally the recognition of substantial behavioural flexibility in copepods renders fossil the notion that copepods are mere automata capable of only hard wired stimulus responses. The development of new, solipsistically defined trophic classes and foraging trajectories provide substantial new approaches to copepod biology and invite scientists of innovative research.

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STRUCTURE, FUNCTION AND BEHAVIOUR, AND THE ELUCIDATION OF EVOLUTION IN COPEPODS AND OTHER CRUSTACEANS

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Abstract: The basic crustacean larva is the nauplius. Adaptive radiation among nauplii has been achieved via both morphology and behaviour. While small size has been an evolutionary constraint, nauplii have also exploited this attribute in ways denied to larger organisms. Copepod nauplii display considerable adaptive radiation but much remains to be learned.

Post naupliar development, whether via anamorphosis, as in the Anostraca, or via metamorphosis, as in the Copepoda, leads to increased mechanical complexity. The available tool kit is extended, new ways of life and patterns of behaviour can be exploited, and more efficient swimming and more elaborate means of food collection become possible.

Crustacean evolution generally involves both morphological and behavioural components. Profound changes in morphology may involve equally profound changes in behaviour, as in the evolution of the complex feeding behaviour of atyid prawns. Physiological changes influencing behaviour may, however, be largely independent of morphology, as in cases of longevity in crayfishes and copepods.

The reasons for some changes in behaviour are difficult to understand. An example is the loss of the ability to swim, and what appears to be a secondarily acquired need to use an intermediate host, by branchiurans of the genus Chonopeltis that have to leave the host to lay eggs. The evolution of spermatophores by Dolops, which involved profound developments in morphology and the acquisition of elegant patterns of behaviour is another.

The basic crustacean larva is the nauplius, so it is appropriate to begin any consideration of behavioural ecology of crustaceans with a consideration of this larva. That the nauplius is, and has been, a successful design is attested by its widespread occurrence in crustaceans of many major taxa and by its long history. From its occurrence in remotely related taxa whose ancestry in some cases goes back to the Cambrian it can be deduced that the nauplius is an ancient larval type. The alternative, and less likely, possibility, is that it has evolved more than once. Confirmation of its ancient nature has come from the fossil record; first from Scourfield's finds of early postnaupliar stages in the Devonian lipostracan Lepidocaris and, more recently and even more dramatically, from Müller's (1981) finds of late Cambrian nauplii. These phosphatised nauplii are immediately recognisable as such, and while one naturally looks for primitive features, the outstanding attribute of these fossils is their similarity to modern nauplii. The nauplius larva is a living fossil.

The abundance of nauplii, another hallmark of success, is also worthy of emphasis. I believe that the nauplius represents the most abundant type of multicellular animal in existence. With the exception of a few parasitic species, all copepods, of which there are probably more individuals in the world than of any other group of animals, begin life as a nauplius, as do other numerous groups, as diverse as barnacles, ostracods (whose nauplius is camouflaged by a bivalve carapace) and euphausids. Nauplii are also found in other groups, such as branchiopods and certain primitive prawns. Some penaeids produce as many as a million nauplii in a single brood.

All nauplii share certain basically similar attributes. They are motile heads with no trunk appendages. All possess but three pairs of appendages - antennules, antennae and mandibles. They are also small - a fact which has an important bearing on their movements, the size of food particles they can handle, and their ecology in general. While it has been the starting point for the development of animals which, either by anamorphosis, as in branchiopods such as the Anostraca, or by metamorphosis, as in the Copepoda, may be very different as adults, the nauplius is more than a mere starting point. It has undergone adaptive radiation in its own right. As we are dealing with a relatively "simple" organism, whose basic plan is readily seen and appreciated, there are considerable opportunities for the analysis of this adaptive radiation.

Changes in body form that have been possible are inevitably of a limited kind, though it is surprising what can be done with an ovoid shape. It can remain plump, as in the nauplii of various, distantly related, animals, or become flattened and discoidal, as in many harpacticoid copepods. Frontal horns can be developed, as in barnacle nauplii, a long posterior spine can be acquired, again seen in certain barnacle nauplii, and, in a more extreme form, in the copepod Longipedia (Gurney, 1930). A dorsal shield can be carried as in the nauplius of the conchostracan Lynceus, or the entire body can be enveloped by a bivalve carapace, as in ostracods.

The morphological changes that can be rung on only three pairs of appendages might also appear to be limited, though some of the things that insects have done with just this number of legs should be a caution here, and the structural and functional diversity of naupliar appendages, exploited by very different kinds of behavioural ecology, have taken nauplii into a wide range of habitats and niches. In the Copepoda alone the diversity extends from planktonic forms that inhabit open seas or the pelagial regions of lakes to those whose universe is no more extensive than the interstitial spaces between sand grains or moss fronds, or is even confined to the spaces within the fronds of a seaweed.

We can already see that adaptive radiation among nauplii is a complex subject and can only be introduced here. As the Branchiopoda include the most primitive of extant crustaceans (though some are very complex) and as some of these begin life as a nauplius, it is convenient to begin our exploration here. The anostracan Branchinecta ferox hatches as a nauplius provided with sufficient yolk to enable the first instar to survive without the need to collect food. This is the limit of parental investment in its offspring. After the first moult the nauplius must fend for itself. The strategy of providing food for the nauplius has been adopted to various degrees by different species and has an important bearing on behavioural ecology. Some nauplii do not feed at all so there is no necessity for the appendages to acquire the ability to collect food. There seems to be little correlation between taxonomy and strategy here. Thus, among the Copepoda, while many nauplii apparently receive little in the way of an endowment of yolk and have to fend for themselves from an early stage, others, certainly among parasitic species where such provisioning is presumably less of a burden on the parent, are well-endowed in this respect and some seem never to feed at all. Such, however, is also the case in at least one free-living species, Euchaeta norvegica (Nicholls, 1934) so all-embracing generalizations cannot be made. Penaeid prawns and euphausids seem also to have non-feeding nauplii - perhaps in this case a character of the group as a whole. Such non-feeding nauplii are in effect free-living embryos; they make no nutritional demands on the environment while development proceeds.

To return to B. ferox, here the mandibles of the first instar are non-functional but a more developed condition is available for use after the first moult when feeding begins. B. ferox displays a remarkable specialization, present during only a single instar, which begins to reveal the potentiality of the nauplius. During the second instar, that part of the mandible which handles food - here small particles - is a stout spine which arises from the posterior margin of the gnathobase. Opposed spines of right and left mandibles sweep particles forward as the mandibles roll in a manner characteristic of the Anostraca, and several other groups of branchiopods. After the next moult these sweeping spines are relatively shorter and merely assist the gnathobases whose molar surfaces are now functional.

From now on, and for several instars, the nauplius swims and feeds in a characteristic way. Swimming is carried out entirely by the antennae which are analogous to the oars of a boat - or the wings of a bird - but the small size of the nauplius leads to enormous differences from those, in certain respects similar, mechanisms. The nauplius inhabits a viscous medium: a low Reynolds number environment as students of small aquatic organisms are now becoming aware. It therefore has no momentum and in effect levers itself through the water. Indeed when the movements of the antennae are analysed it transpires that, although they have a wide amplitude of beat, their tips actually swing posteriorly for only a short distance during a cycle of movement. At the end of the stroke, forward movement of the nauplius stops, and indeed during the return phase it actually moves backward a little, at least in early instars.

The same cycle of movement enables the nauplius to feed. Previous accounts of feeding by branchiopod nauplii have attributed the collection of particulate food to the natatory setae of the exopodite of the antennae, but this is not so. Apart from the fact that, even if they collected particles, these setae have no means of passing them to the mouth, as we have seen, they do not move very far through the water. Their function is to propel not to sieve, and the two functions are incompatible: propelling setae are not good sieves and a sieve would not be a good propulsive organ. Food is in fact collected by specialized spines on the antennae which, in spite of the limited backward movement of these appendages sweep through a considerable volume of water during one part of the cycle. Material so collected is passed to the mouth. Details of the process are described elsewhere (Fryer 1983) and need not detain us here.

The processes so briefly described, whose morphological features are readily apparent, naturally demand a suitable musculature for moving the appendages, sensory receptors for receiving relevant information, and a nervous system capable of the necessary co-ordination. Simple as they appear to be on casual acquaintance, nauplii are in fact anatomically complex - indeed the musculature of the antennae of B. ferox is more complex than that of many malacostracan appendages, and co-ordination is of a high order.

Some time has been spent on the nauplius of Branchinecta for several reasons. Being the nauplius of one of the most primitive of extant crustaceans it might be expected to reveal primitive features; it reveals the complexity of naupliar organisation, which seems not to have been generally appreciated, and it corrects erroneous impressions as to how anostracan nauplii feed.

While essentially similar in basic structure, copepod nauplii differ much from those of branchiopods in their locomotion and, particularly, their feeding mechanisms. While we are gradually accumulating good accounts of naupliar morphology and development in copepods - e. g. there have been recent excellent and welcome publications on the development of harpacticoid nauplii (Carter and Bradford 1972; Sarvala 1977a,1977b; Schminke 1982), detailed accounts of copepod naupliar anatomy and feeding mechanisms are still needed. It is clear, however, both from general observations and especially from the work of Gauld (1959) that copepod nauplii collect food predominantly with the mandibles and pass it mechanically towards the mouth, in which process they are aided by the coxal spine or spines of the antennae. There are enormous possibilities for comparative studies here, for example between calanoid, cyclopoid and harpacticoid nauplii with their different anatomies and ways of life. Even within one major group there are great differences in ecology, habits and abilities, and one might reasonably expect to find differences in the feeding habits of, for example, the freely swimming nauplii of Canthocamptus staphylinus and their creeping Sphagnum-frequenting equivalents in Moraria brevipes or interstitial space-inhabiting species of Parastenocaris.

Some hint of what we can expect when copepod nauplii are better studied is given by Harding's (1954) work on the harpacticoid Thalestris rhodymeniae. The minute nauplii of this species (the stage I nauplius is only about 90 µm, in length) which lives within the fronds of the seaweed Rhodymenia palmata on which it and the adults stimulate the production of galls, are almost spherical in shape. The antennae possess remarkable, stout, evidently biting, mandible-like gnathobases that look so much like mandibles that, seen in isolation, they would be unhesitatingly - but erroneously - identified as such.

As the development of nauplii proceeds, additional appendages become available for use. The tool kit is extended. Increased complexity offers increased opportunities for diversification. One can do more with an elaborate set of tools than with just a hammer and chisel. In Branchinecta appendages are added gradually to the naupliar complement, a primitive arrangement; locomotion is gradually taken over from the antennae by thoracic limbs, and food collection also becomes the responsibility of these limbs though the final handling is still carried out by the cephalic appendages. Other branchiopods, which may or may not have an active nauplius, retain the antennae as organs of locomotion while the trunk limbs become specialised for food collection. In Branchinecta too the mandibles undergo what are functionally only minor changes from the nauplius to the adult and the same basic musculature is used throughout, though of course it becomes more robust with increasing size.

In copepods the change is more abrupt at the metamorphosis from last naupliar to first copepodid stage, and essentially adult food handling apparatus is acquired in free-living species. Functional changes are sometimes drastic. For example the antennae loose their coxal spines and no longer help to pass food to the mouth, and the mandibles change markedly to assume an essentially adult form quite different from that of the nauplius. Often the cephalic appendages cease to contribute to locomotion, which function is taken over by the thoracic limbs.

It is at this stage of the life cycle that divergence between free-living and parasitic copepods sometimes becomes clearly apparent. This is so for example in the Cyclopoida. The copepodids of free-living species require mouthparts suited to the collection of appropriate items of food which can be seized and manipulated: those of Lernaea, mouthparts suitable for feeding, usually on the gills, of a host fish. This difference was almost certainly initiated by a change in behaviour. Many cyclopoid copepods are predators, sometimes attacking even small fishes. Such habits were probably the precursors of semi-parasitic, and eventually entirely parasitic modes of life.

Evolution in the Crustacea generally involves both morphological and behavioural components. Sometimes dramatic steps can be taken as a result of changes in behaviour that involve only small morphological changes. The colonization of the pelagic waters of lakes by cyclopoid copepods is an example. At the other end of the spectrum are changes in morphology which involve scant changes in general behaviour but which drastically alter the animal's way of life. Such is the case in the anostracan Branchinecta ferox which, in middle age, loses the filtratory setules of its trunk limb setae. This puts an end to its life as a filter feeder and it becomes a carnivore, feeding chiefly on calanoid copepods in the one area where it has been studied, but the mechanisms of food collection and food handling remain essentially unchanged.

More usually both aspects are involved and can be of unexpected and unpredictable kinds. Examples of which I have personal experience are the parasitic habits of chydorid cladocerans of the genus Anchistropus and the remarkable feeding habits of atyid prawns. Anchistropus belongs to a group of otherwise free-living and mostly microphagous, (often, but not always, filter-feeding) animals, yet has become parasitic on Hydra over whose body it climbs, ripping out pieces as it does so, and against whose stinging nematocysts it has evolved protective devices. Although such a way of life has called for remarkable, in several cases unique, morphological adaptations, such as an armour-plated food groove, special devices for clinging to and clambering over the body of the host, and many modifications of the food-handling appendages, these would have been useless without profound modifications of ancestral behaviour patterns. Even when it is appreciated that the ancestors of Anchistropus may have been pre-adapted to life on Hydra by having a thick carapace cuticle and limbs which, as in Pseudochydorus, were probably already modified for handling large lumps of material (dead bodies are shovelled and forked in Pseudochydorus) the changes in behaviour that led to the filling of this entirely new ecological niche are truly remarkable and could scarcely have been predicted.

Equally remarkable are the feeding habits of atyid prawns. Had not such organisms existed, the idea that an animal like a lobster might begin to use its chelipeds as filtering appendages would be treated with ridicule, yet that is what some atyids do with theirs. Several species have chelipeds fringed by elaborate and beautifully adapted scrapers and brushes and scrape finely particulate material from surfaces. Others, such as Atya and Micratya, can both whisk up such material or collect it passively by spreading long fringing setae of the four chelipeds, each of which makes a filtering cup, fitting all four together to make a superb filtering network, and extending this complex array to face an oncoming current from which particles are extracted. These are then transferred to the mouthparts, themselves highly elaborate (Fryer, 1977). Again the morphological changes involved during the evolution of such a device are mind boggling, but the changes in behaviour are equally profound - again think of the unlikelihood of a lobster holding up its chelipeds in a stream - and have enabled atyids to fill new ecological niches. Similar profound changes in both morphology and behaviour are familiar to students of parasitic copepods.

The changes in behaviour to which we have so far referred have gone hand in hand with changes in morphology, but other changes of behaviour, which can have important evolutionary consequences, may be largely or entirely independent of morphology and be related to physiological changes that enable animals to colonise new environments or exploit already occupied environments in different ways.

Some of the most interesting of such changes are related to longevity. Cooper's work on the cavernicolous crayfish Orconectes australis (cited by Culver, 1982) suggests that the growth rate is so slow that individuals with an average rate of growth do not reach a reproductive size until they are about 105 years old and that those growing at the average rate for the cave studied would take 176 years to achieve maximum size. These figures could be lower for 'fast' growing individuals - but some grow slower than this!

Although the periods are shorter, when the size of the organism is taken into account the life spans of certain harpacticoid copepods are equally remarkable. Rouch (1968) has shown that the adult stage of the subterranean Bryocamptus pyrenaicus can live for almost 20 months, but more startling are the observations of Schminke (1982) on Parastenocaris vicesima. A single adult female of this species was kept in captivity for 2 1/2 years before the first nauplii appeared. As Schminke says, it is remarkable that sperm remained viable for so long, and indeed he naturally suspected parthenogenesis though he tended to discount this as some of the nauplii eventually produced adult males. Taking into account the 6 months or more spent in the larval stages (as shown by Schminke's rearing of these) the female must have had a life span of more than 3 1/2 years. How much more it is not possible to say because its age when collected, as an adult, was not known.

The longevity of cavernicolous crayfish and copepods has been attributed to life in an environment where food is scarce (Culver, 1982), but this can scarcely apply to Parastenocaris, species of which have interstitial habits, and it is difficult to believe that such habitats are lacking in food for microphagous species such as harpacticoid copepods. Certainly such copepods can be very abundant in the interstitial habitats of sandy beaches of lakes.

Likewise a shortage of food can hardly be the cause of longevity in planktonic Cyclops scutifer in a temperate lake in Norway where Elgmork (1981) found some individuals to have a life span of three, in some cases possibly four, years. Here the life cycle is prolonged by two (perhaps in some cases three) periods of diapause, but these are in winter when metabolic rates would in any case be low, and the various developmental stages are active in summer when temperatures can reach 20°C. In planktonic copepods in general, both marine and freshwater, the life span does not usually exceed one year except in a few Arctic and sub-Arctic species where low temperatures prevail even in summer.

Thus there are several cases among copepods in which changes in behaviour related to life-spans have occurred, and which presumably have ecological repercussions.

There are also interesting and challenging cases where changes in behaviour appear to be virtually inexplicable. The Branchiura provide several examples. Members of the genera Argulus and Dolops can swim well both as adults and as juveniles irrespective of whether the latter are modified nauplii or juvenile adults. Such an ability would appear to be of great importance to these genera. Females, which are parasitic on fishes, have to leave the host in order to deposit their eggs on firm substrata - an unusual habit in the Crustacea as a whole and one to which we shall return. If they wish to resume their parasitic way of life they must find a new host. An ability to swim well would appear to be essential for this and, to judge from the size range of mature females of several species that can be found on a host, such a resumption of parasitic habits is common. The young also need to find a host quickly, and proficiency in swimming is an obvious asset. I think it is legitimate to assume that an ability to swim is a primitive attribute of the group. It is surprising, therefore, to find that in the African genus Chonopeltis neither the adult nor the larval stages can swim. Adults of several species have been seen alive and in no case can they do more than move laboriously over the host by 'walking' movements of the maxillary suckers. The anatomy of species known only as preserved specimens shows clearly that they suffer the same restrictions. Nevertheless females leave the host to oviposit. Eggs have been laid in captivity, and larvae (incidentally of a type unique in the Crustacea) have been hatched and their activities observed (Fryer, 1956). Not only are they unable to swim but they are singularly inept at moving about. As if this was not a sufficient handicap in life, at least one species employs an intermediate host (Fryer, 1961) something that, so far as I am aware, is not reported for any species of Argulus or Dolops. Transmission seems to depend on contact being made with a bottom-frequenting fish. What can be the selective advantage of either the loss of the ability to swim or the incorporation of an intermediate host into the life cycle?

The Branchiura present other intriguing evolutionary problems involving both structure and behaviour. Of the former the evolution of suckers is one, but we are concerned with behaviour. Branchiurans lay their eggs on firm substrata. This in itself seems to be a somewhat hazardous undertaking for an entirely parasitic group, and the route to its evolution is fascinating to contemplate. As a guess I would suggest that such egg-laying habits, which may have been related to a morphology that made it inconvenient either to store eggs in a pouch or carry them in an external sac, arose before the group adopted parasitic habits, and that they were committed to it from the outset of their career as parasites. It would be an odd strategy for already established parasites to adopt. Among crustaceans as a whole it is indeed a rare method of dealing with the eggs, though some ostracods practice it. One wonders why this should be so when so many insects including both those which are fully aquatic and those with aquatic stages, as well as mites, employ it.

In Argulus and Dolops egg-laying involves the pricking of each egg by hollow spikes down the duct of which sperms pass from spermathecae in which they had previously been stored following mating. In Argulus, sperm is transferred directly from male to female. Dolops, however, employs a spermatophore. As the kind of spermatophore employed makes use of the egg-pricking spikes it could not have evolved before they had come into use. Thus the spermatophore is a derived, and not a primitive, character. What were the advantages of its evolution? That the primitive, or ancestral device employed by Argulus is successful can be adduced from the fact that many species of this virtually world-wide genus employ it, and from its inferred antiquity. That the derived condition of using a spermatophore is sufficiently ancient to have evolved prior to the break-up of Pangea is shown by the distribution of the genus Dolops - Africa, S. America and Tasmania. The system employed by Argulus must be of even greater antiquity and has proved successful. What then was the stimulus to produce a spermatophore, and how does one start to produce such a thing? Dolops today has striking morphological specializations for the making of its spermatophore - elaborate spermatophore glands for the secretion of the wall material, canals and vesicles for the conveyance and storage of this material - and has evolved remarkable specializations in behaviour that come into play at the time of spermatophore transfer. The wall material, enveloping a blob of sperm, is extruded as a bubble (its shape being determined by physical forces) and kicked free as a completely closed sphere. This is then impaled upon the spikes at the end of the spermathecal ducts of the female which penetrate its thick wall and enable the sperms to pass from the otherwise sealed spermatophore to the spermathecae. After a moult, which gets rid of the now empty spermatophore, the spikes can be used to prick, and inject sperm into, the eggs as in Argulus. The stimulus to the evolution of such a radical departure from the ancestral condition and the complex changes in morphology and behaviour involved present many challenges - as indeed does the evolution of the curious behaviour of egg pricking. With these and many other problems to tease his wits, the student of behavioural ecology is unlikely to run out of things to do in the immediate future.

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THE COMPARATIVE ANATOMY OF THE FEEDING APPARATUS OF REPRESENTATIVES OF FOUR ORDERS OF COPEPODS

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Abstract: The skeletomusculature of the feeding appendages and the gross morphology of the digestive tract of calanoid, mormonilloid, misophrioid and siphonostomatoid copepods are compared. The five species studied each represent a different feeding strategy; predatory (Euaugaptilus), gorging (Benthomisophria), filter feeding (Mormonilla), micropredatory (Hyalopontius) and parasitic (Lepeophtheirus). Feeding mechanisms are postulated for these copepods and an attempt is made to identify any general patterns in skeletomusculature and gut morphology associated with each feeding strategy.

INTRODUCTION

Great advances in our understanding of copepod feeding mechanisms have occurred in recent years due primarily to careful observations of living animals (Fryer, 1957; Marcotte, 1983) and to the techniques of high speed cinematography (Price et al., 1983). Anatomical studies have been few during this period yet knowledge of musculature and joint structure greatly facilitates functional interpretation of the feeding appendages. The present account comprises a comparison of the skeletomusculature of five copepods having different feeding strategies and is intended to complement studies on live copepods.

FEEDING MECHANISMS

1. Euaugaptilus Sars

The calanoid Euaugaptilus is a large and powerful predator which probably feeds mainly on other copepods. It swims slowly by means of its antennae and mandibular and maxillularly palps which have plumose setae adapted for producing water movement. Once the prey is within reach it can be caught in either of two ways: the predator can use its maxillae and maxillipeds raptorially and grasp the prey directly with the tips of its setae (the 'chopsticks' method of Alcaraz et al., 1980) or it can perform a 'maxillary fling' to capture a parcel of water containing the prey, as described by Koehl and Strickler (1981). In this latter case the maxillae are rapidly abducted and extended, spreading the maxillary setae and drawing in towards the copepod a parcel of water containing the prey. The maxillae are then adducted and flexed, pulling their setae through an arc in towards the midline. The prey is grasped as the water enclosed with it is squeezed out through the mesh of setae. In either method the prey is actually grasped by the 'button' setae of the maxillae, probably assisted by those of the maxillipeds. The stalked buttons are modified setules which serve to increase the surface area of the seta coming into contact with the prey and to protect the primary feeding setae by acting as buffers, absorbing some of the energy of the struggling prey.

The prey is passed forwards mechanically to the arthrite of the maxillule, the setae of which are armed with stud-like denticles which improve their grip on the prey as they pass it on to the mandibles. The mandibular gnathobase is elongate and has slender teeth. It is used to pierce and cut the prey into fragments before ingestion.

2. Benthomisophria Sars

The misophrioid Benthomisophria palliata Sars is an opportunistic macrophage, adapted for gorging. When fully gorged the midgut is grossly distended occupying virtually all the free space within the prosome. It is suggested that the maxillae and maxillipeds are used for grasping the prey directly, as in the predatory cyclopoids described by Fryer (1957), because of the arrangement of the mouthparts (see below) and because the anterior appendages are not involved in generating feeding currents as they are in Euaugaptilus. Prey are passed forwards to the mandibles mechanically by the maxillulary arthrites. The feeding mechanism is quite typical of predatory podopleans but the extent of the adaptations to macrophagy is remarkable in Benthomisophria. The integument of the first pedigerous somite is flexible and loosely folded to allow for the dorsal and lateral distension of the midgut. This somite is protected by a carapace-like extension of the preceding somite which encloses it dorsally and laterally. As suggested elsewhere (Boxshall, 1982) the presence of areas of secretory cone organs on the sides of the dorsal shield and the reflexed configuration of the antennae and mandibular palps are both linked to the presence of this carapace. Distensibility of the midgut has also had repercussions on internal organ systems. B. palliata has lost its heart, which would have been in the middle of the prosome where greatest distension takes place. Similarly, adult misophrioids retain antennary glands as their excretory organs rather than the typical maxillary glands as this provides a means of displacing organs from the middle of the prosome. These unique misophrioid characters collectively represent the morphological impact of adopting gorging as a feeding strategy.

3. Mormonilla Giesbrecht

Mormonilla is the only genus of the order Mormonilloida and its two species are mesopelagic filter feeders. One of the most striking external features of Mormonilla is the relatively enormous filter basket occupying nearly a third of the body length. The lateral and ventrolateral walls of the filter basket are formed by the long setae of the mandibular and maxillulary palps. The exopodal setae of both are plumose, adapted for generating water currents as their close set setules prevent water passing through the intersetule spaces. The widely spaced setules of the endopodal setae allow water to pass through but prevent the passage of particulate matter. These setule rows are set at an angle of about 120° to each other so that the tips of setules from adjacent setae interdigitate thereby helping to maintain the integrity of the large area of mesh. The antennary exopod helps to close the filter basket laterally and the endopod midventrally. The first swimming legs close it posteriorly.

A parcel of water containing food particles is enclosed by the remotor swing of the anterior mouthparts and by the promotor swing of the first legs. As the basket closes some of the enclosed water will be forced through its walls but loss of food particles is probably insignificant. The maxillae lie within the filter basket and can be swept through the enclosed water. The distal maxillary setae have rows of long setules which interdigitate with the peg setules of the adjacent setae to make the filtering apparatus more robust. As the maxillae are adducted food particles would be retained on the grid of maxillary setae despite the effect of boundary layers in the highly viscous environment because the water is confined in the basket. The maxillipeds also lie within the basket but differ in their armature. They may assist in removing particles from the maxillae and in passing them forwards as the maxillipedal setae extend as far as the labrum where they can be groomed by the mobile maxillulary arthrite. The toothed margin of the mandibular gnathobase is typical of particle feeders and differs from the cutting gnathobase of Euaugaptilus.

4. Hyalopontius Sars

The siphonostomatoid Hyalopontius contains eight species all of which have been taken in plankton nets, at depths from 2,000 to over 4,000 m. None has ever been found in association with a 'host' and all have well developed swimming legs. It is probable that these forms attach temporarily to their host (prey) whilst feeding and can thus be regarded as micropredators. Under the name Megapontius Hulsemann this genus has attracted much attention (Gotto, 1979; Kabata, 1979 and 1981) and Heptner (1968) published a preliminary study of the structure of its oral cone. Although retaining some primitive features, Hyalopontius is typical of siphonostomes as a whole and is used as a basis for comparison.

When Hyalopontius encounters a prey it grasps it using the maxillae, maxillipeds and, to some extent, the antennae. These limbs have relatively loose basal articulations and are capable of extensive whole limb movements. The maxillae and maxillipeds have powerful distal claws for grasping and holding the prey and they have only to hold the copepod onto its prey to enable it to feed using its oral cone. This consists of the anterior labrum and posterior labium which are confluent where their bases meet lateral to the mouth but remain entirely separate distally, as in other siphonostomes. Scanning electron micrographs of the oral cone (Figure 1A) show the labrum wrapping round the edges of the labium distally but there is no fusion between them. The flared distal opening to the oral cone is labial in origin. The siphonostome mandible is reduced to a stylet-like gnathobase and a small uniramous palp. Hyalopontius, like many others, lacks the palp. The mandibles are located lateral to the oral cone and pass obliquely into it via the slit separating labrum from labium. The tips of the mandibles enter the central cavity of the oral cone distally. The cavity is homologous with the preoral cavity of non-siphonostomes and is referred to here as the buccal cavity. In Hyalopontius the inner lobe of the maxillule also passes medially into the oral cone but never enters the buccal cavity. It lies in a groove in the labium enclosed by overhanging flap of the labrum and its apical setae emerge distally around the oral cone opening. A similar arrangement occurs in Entomolepis Brady, a form with an extremely long oral cone, in which one seta on the inner maxillulary lobe runs the entire length of the cone.

5. Lepeophtheirus von Nordmann

Lepeophtheirus pectoralis (O.F. Müller) is a caligid siphonostome which attaches to its flatfish hosts by means of subchelate antennae and maxillipeds. The maxillae appear to be grooming appendages in the caligiform families. The oral cone is similar in structure to that of Hyalopontius although both labrum and labium form the distal opening of the cone. The stylet-like mandible passes obliquely into the buccal cavity but the maxillule is reduced to a small papilla bearing three sensory setae and a stout posterior process, neither of which enters the oral cone. As the copepod moves over its host the oral cone is held in a posteriorly-directed position and it must be erected perpendicular to the body before feeding. It is erected by two pairs of muscles which originate on the postmaxillulary apodemes and pass forwards to insert on the paired buccal apodemes (Figures **1b** and **3**). The epidermal tissues of the host are abraded by the action of the mandible and labial strigil, as described by Kabata (1974).

EXTRINSIC MUSCULATURE OF THE CEPHALOSOMIC APPENDAGES

The most striking feature of the extrinsic musculature of Euaugaptilus is its complexity. There are large numbers of dorsal and ventral muscles moving the appendages, each of which performs several functions and is capable of a range of movements. The antennules are sensory and play a steering and stabilizing role during locomotion. The antennae produce water currents as a part of the feeding mechanism and are involved in grooming. The mandibles and maxillules produce water currents with their palps and transfer and fragment the prey with their gnathobases. The maxillae and maxillipeds perform a range of raptorial and manipulative movements during prey capture and handling. It is this functional multiplicity which explains the complexity of the musculature. No single functional role is dominant so, whilst the muscles exhibit a range of sizes (in terms of cross-sectional area), no muscles are grossly better developed than the others. Epilabidocera amphitrites McMurrich, an omnivorous calanoid, exhibits a similar overall complexity (Park, 1966).

Benthomisophria has fewer muscles than Euaugaptilus. Both are predatory and the common requirement for grasping and manipulative movements during prey capture and handling determines the similarities in musculature of the postmandibular limbs. The differences between these genera are related mainly to the increased importance of the reflexed antennae and mandibular palps in Benthomisophria. These appendages are involved in grooming the carapace and their muscles are the most powerful in the head. Their size clearly represents a considerable anatomical investment.

Calanus Leach has been regarded as the typical example of copepod filter feeding and the close similarity in musculature between Calanus (as described by Perryman, 1961) and Euaugaptilus is unexpected. However, the newly emerging model of calanoid feeding behaviour, based largely on the elegant studies of Strickler and his coworkers (Alcaraz et al., 1980; Koehl and Strickler, 1981; Strickler, 1982; Price et al., 1983), suggests that particle feeding and predation can be essentially the same process in calanoids. Medium and large sized particles and prey items can all be captured by the maxillary fling method. Very small particles are treated in a different way (Price et al., 1983) and grasping prey directly with the setae of the raptorial appendages is another distinct process. The maxillary and maxillipedal muscles are more powerfully developed in Euaugaptilus than in Calanus because these limbs must grasp and hold large prey.

The basic gnathostomatous mouthparts found in all three of these copepods can be used for particle feeding and for predation. The ancestral copepod was probably a generalist with gnathostomatous mouthparts and their relatively complex musculature is probably also an ancestral condition. The simple musculature of Mormonilla is thus regarded as a derived condition. Mormonilla is a highly specialised filter feeder which uses its anterior mouthparts and its swimming legs to form an enormous filter basket. The main movement of its antennules, antennae and mandibular and maxillulary palps.is a simple promotor-remotor swing about a slightly oblique pivot line (see Figure **2b**). Each of these appendages has antagonistic promotor and remotor muscles although the latter two also have adductors and abductors for their gnathobases. Only the maxillae and maxillipeds have the capacity for more complex twisting movements and even for these the range of movements is small. The marked reduction in numbers of muscles has led to the loss of the posterior cephalic tendon and to changes in

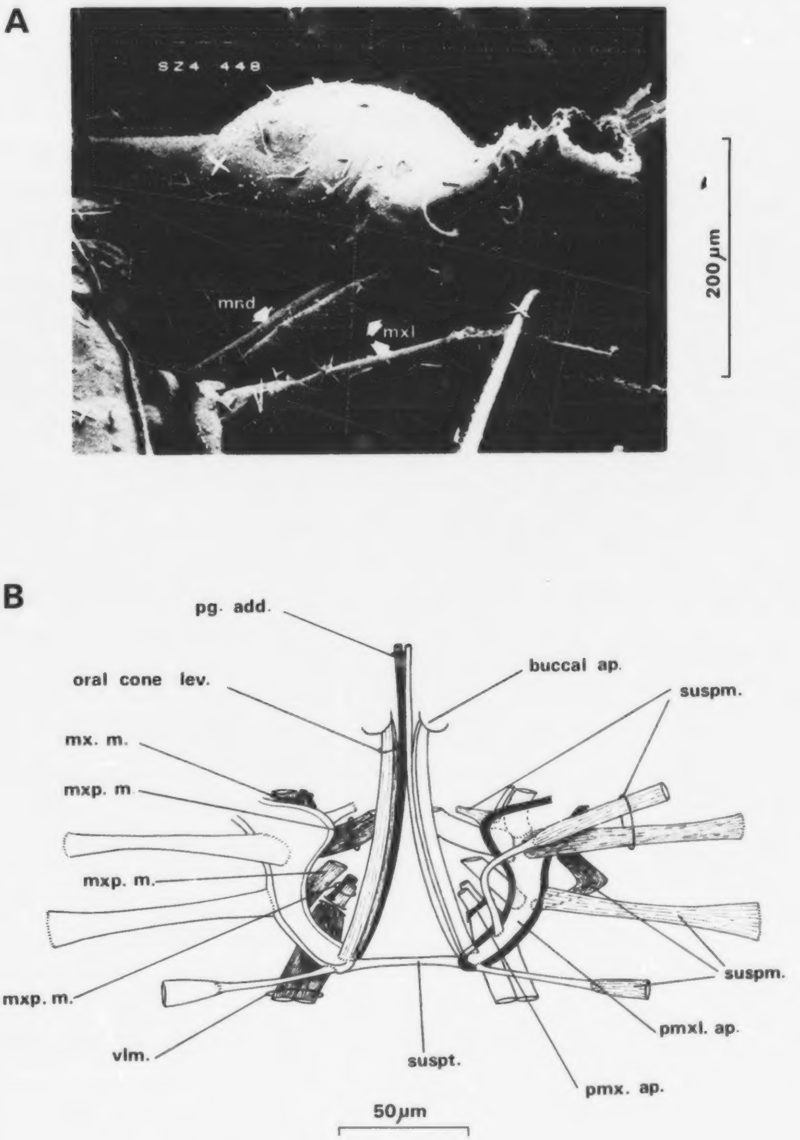
A
SZ4 448
mnd
mxl
200µm
B
pg. add.
oral cone lev.
buccal ap.
suspm.
mx. m.
mxp. m
mxp. m.
mxp. m.
suspm.
pmxl. ap.
vlm.
suspt.
pmx. ap.
50µm

Figure 1. ***A**, S.E.M. micrograph of the oral cone of H. typicus, lateral view; **B**, Semidiagrammatic dorsal view of ventral cephalosomic limbs muscles and apodemes of P. abyssicola (♀), reconstructed from serial sections. Abbreviations: add - adductor, ap - apodeme, lev - levator, mnd - mandible, mx - maxilla, mxl - maxillule, mxp - maxilliped, pg - paragnath, pmx - postmaxillary, pmxl - postmaxillulary, suspm - suspensory muscle, suspt - suspensory tendon, vlm - ventral longitudinal trunk muscle.*

the site of origin of some remaining muscles.

Hyalopontius also has fewer dorsal extrinsic muscles than Euaugaptilus and its ventral muscles are considerably reduced. The posterior cephalic tendon is lost and the small anterior tendon provides a site of origin for only four pairs of mandibular muscles. A few ventral muscles to postmandibular limbs originate on the postmaxillulary and postmaxillary apodemes. The dorsal muscles of the antennae and maxillipeds are well developed and produce the whole limb raptorial movements for grasping the prey. The distal claws of the maxillae and maxillipeds are operated by intrinsic flexor and extensor muscles. The flexors have short fibres and insert onto a rigid apophysis which extends proximally from the joint into the syncoxa, whereas the extensors insert directly onto the rim of the claw.

There is further reduction of the ventral extrinsic muscles within the siphonostomes. Pontoeciella Giesbrecht, another free swimming planktonic form, has lost both cephalic tendons and most of its remaining ventral muscles originate on the enlarged postmaxillulary apodeme (Figure 1B). Neither the mandible nor the maxillule have any ventral extrinsic muscles. Lepeophtheirus is similar, no cephalic tendons remain and the few ventral muscles originate on the apodemes. Two factors contribute to the general reduction in numbers of extrinsic muscles in siphonostomes. Firstly, there is the loss of adduction-abduction movements of the mandible and maxillule associated with the development of the oral cone and a piercing and sucking mode of feeding. Secondly, siphonostomes catch their prey or host raptorially with their clawed appendages, they do not use the more elaborate maxillary fling method by which many calanoids extract their food from their viscous low Reynolds number environment.

ARRANGEMENT OF THE MOUTHPARTS

It is possible to detect some patterns in the arrangement of the mouthparts on the ventral surface of the cephalosome relative to each other and to the position of the mouth which appear to be related to feeding biology. Euaugaptilus (Figure 2A) and Calanus (Perryman, 1961) exhibit a typical calanoid pattern in which the mouthparts are arranged linearly, either side of the mouth, but with the rows curving medially at the level of the maxillae and maxillipeds. Mormonilla (Figure 2B) has a similar linear arrangement but has a relatively wider gap between the posterior ends of the rows. In Mormonilla the first legs close off the filter basket posteriorly and perhaps the mouthpart rows should be extended posteriorly to include them, which would then join the rows medially. In both calanoids and mormonilloids the feeding process involves the anterior mouthparts or palps in generating water currents and food items can be captured by the maxillary fling method. Those groups employing this feeding process have an open linear or linear-hook configuration of the mouthparts. Hyalopontius (Figure 2C) has angled mouthpart rows which meet in the ventral midline behind the mouth. In this form the raptorial appendages grasp the prey and hold onto it so that the oral cone is in contact with the host. The anterior mouthparts are not involved in generating feeding currents and the closed, angled configuration of the mouthparts is in this case linked with true raptorial feeding. Benthomisophria (Figure 2D) also has a closed, angled configuration of the mouthparts and its anterior mouthparts, which are reflexed over the carapace, are not involved in generating feeding currents. This is interpreted as evidence that Benthomisophria grasps its prey directly with its maxillary and maxillipedal setae in the manner of a raptorial feeder.

Two other structures play an important role in the feeding process, the labrum and the paragnaths. In addition to its mechanical function of enclosing the mouth anteriorly the labrum

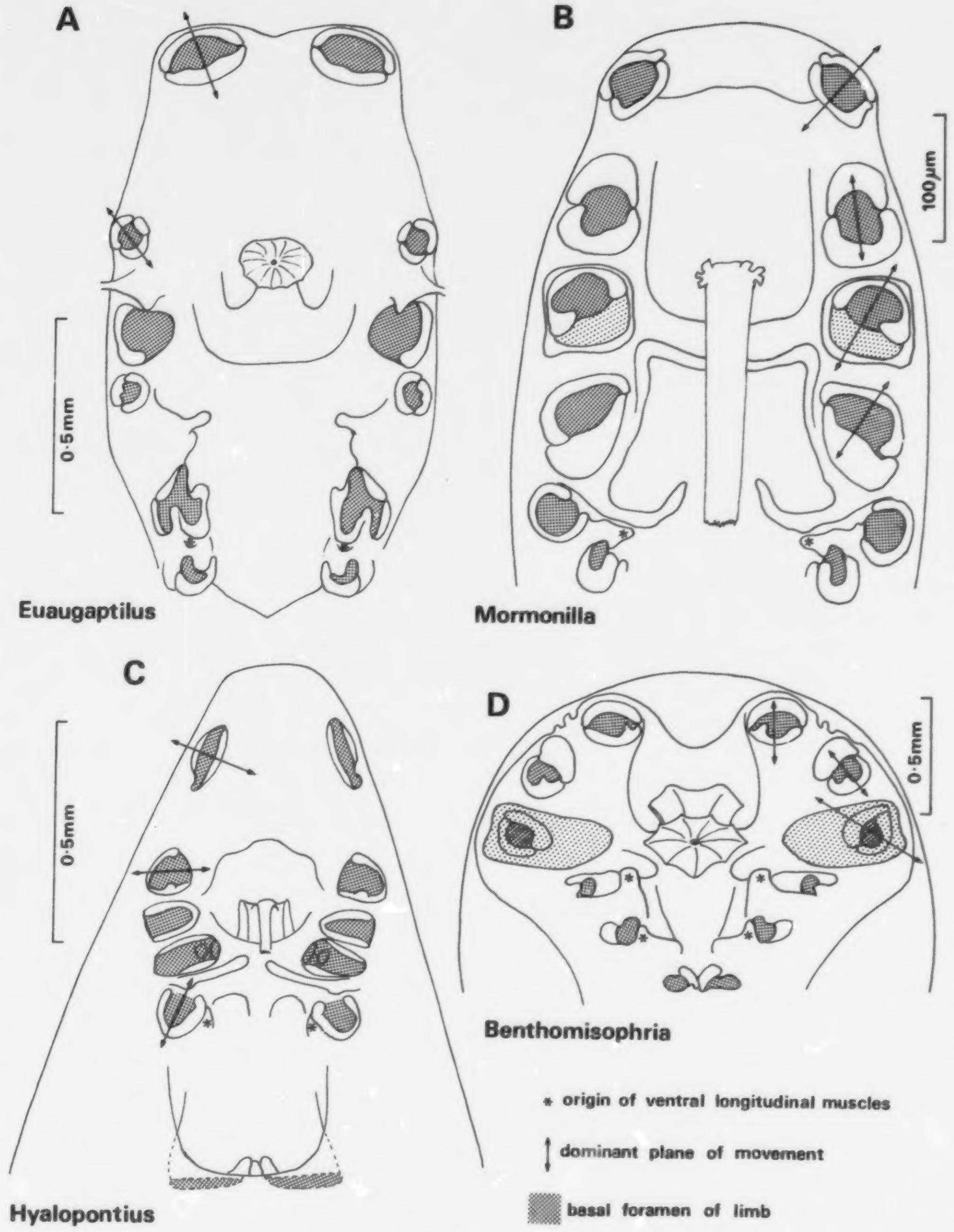
A
Euaugaptilus
0·5mm
B
Mormonilla
100 μm
C
0·5mm
Hyalopontius
D
0·5mm
Benthomisophria
* origin of ventral longitudinal muscles
↕ dominant plane of movement
▨ basal foramen of limb

Figure 2. *Internal views of cephalosome with tissues removed, showing the basal foramina of the limbs of* *__E. placitus__* ***(A)***, *__M. phasma__* ***(B)***, *__H. typicus__* ***(C)*** *and* *__B. palliata__* ***(D)***.

contains secretory glands which discharge their contents onto the food just before it enters the mouth. A large inflated labrum appears to be associated with filter feeding on particulate matter and is found in many primitive crustaceans. *Mormonilla* has a labrum of this type. Predatory copepods, like *Euaugaptilus*, tend to have a smaller, highly muscular labrum although in *Euaugaptilus* the ventral body wall anterior to the labrum is considerably inflated. Development of the labrum reaches its peak in the siphonostomes, in which, together with the labium, it forms the oral cone.

Most copepods have a pair of paragnaths, each of which is a simple lobe located between the bases of the mandible and maxillule. The paragnaths may be capable of some adduction (Fryer, 1957) and in *Benthomisophria* their adductor muscles originate on the ventral surface of the anterior cephalic tendon (Boxshall, 1982). These adductors pass anteroventrally through channels in the suboesophageal ganglion before inserting. In *Euaugaptilus* the paragnaths are highly sclerotised and reduced to low ridges incapable of movement, but they have retained their adductor muscles, which probably serve as suspensors of the cephalic tendon. Siphonostomes lack paragnaths but possess a large labium forming the posterior lip of the oral cone. The conclusion that the labium represents fused paragnaths is confirmed by examination of the musculature. In *Hyalopontius* the labium has an unpaired median muscle and a pair of lateral muscles, all of which originate ventrally on the anterior cephalic tendon and pass through channels in the suboesophageal ganglion before inserting. The pair of muscles inserts apically in the labium and is presumably responsible for movement on the flared distal membrane surrounding the oral cone opening. The median muscle inserts proximally on a tendinous sheet which may represent the plane of fusion of the two paragnaths.

The siphonostome labrum (Figure 3) is packed with muscles which dilate the buccal cavity producing suction pressure to draw food (mainly fluids) in towards the oesophagus which begins at the base of the oral cone. Food is drawn along the oesophagus and into the midgut by peristalsis. At the base of the oral cone is a pair of hollow invaginations off the buccal cavity. These extend dorsally into the head and are referred to as buccal apodemes. In those siphonostomes with erectable oral cones, such as *Lepeophtheirus* and *Pontoeciella*, the levator and depressor muscles insert apically on these buccal apodemes. In both these genera the levators lie parallel to the oesophagus and have their origins on the enlarged postmaxillulary apodemes (Figures 1B and 3). There are two pairs of levators which pass with the oesophagus through the nerve ring formed by the cerebrum, circumoesophageal commissures and suboesophageal ganglion. In transverse section (Figures 4C and 4B) a close similarity between the caligiform *Lepeophtheirus* and the cyclopiform *Pontoeciella* can be seen. This constitutes a clear homology linking fish and invertebrate parasitic siphonostomes together as advanced siphonostomes. The plesiomorphic *Hyalopontius* lacks levator muscles for its oral cone but it possesses a pair of short muscles, serving as oesophageal dilators, which originates dorsally on the anterior cephalic tendon and passes through the nerve ring (Figure 4A) before inserting on the wall of the oesophagus. It is possible that the levator muscles of advanced siphonostomes are derived from these oesophageal dilators.

GROSS MORPHOLOGY OF THE DIGESTIVE TRACT

The small diameter of the nerve ring of siphonostomes allows only limited dilation of the oesophagus (Figure 4) and most feed on fluids and finely fragmented tissues. *Hyalopontius* and *Pontoeciella* both possess a flared membrane surrounding the oral cone opening which when closely

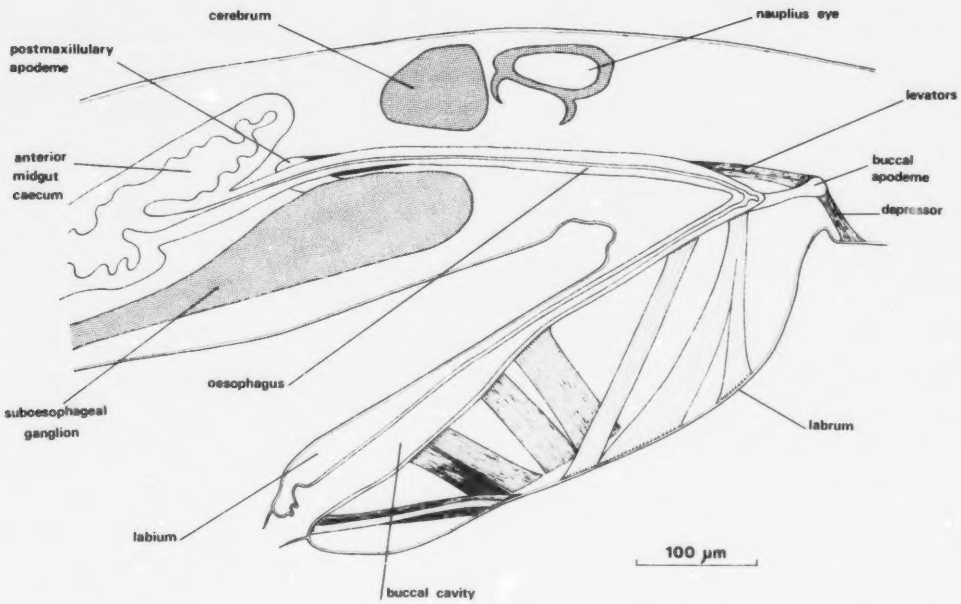
cerebrum
nauplius eye
postmaxillulary apodeme
levators
anterior midgut caecum
buccal apodeme
depressor
suboesophageal ganglion
oesophagus
labrum
labium
100 µm
buccal cavity

Figure 3. *Longitudinal section through oral cone of L. pectoralis, showing the internal musculature of the cone and its depressor and levator muscles.*

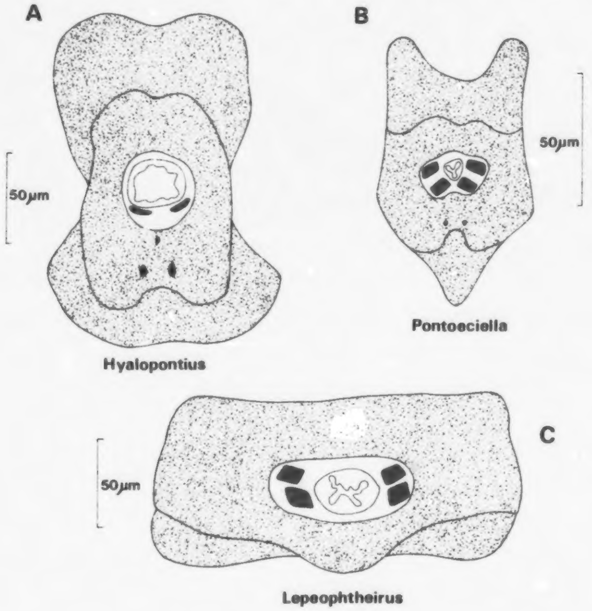
A
50µm
Hyalopontius
B
50µm
Pontoeciella
C
50µm
Lepeophtheirus

Figure 4. *Transverse sections through the nerve rings of H. typicus (A), P. abyssicola (B) and L. pectoralis (C), showing the oesophagus and its associated muscles passing through the nerve ring.*

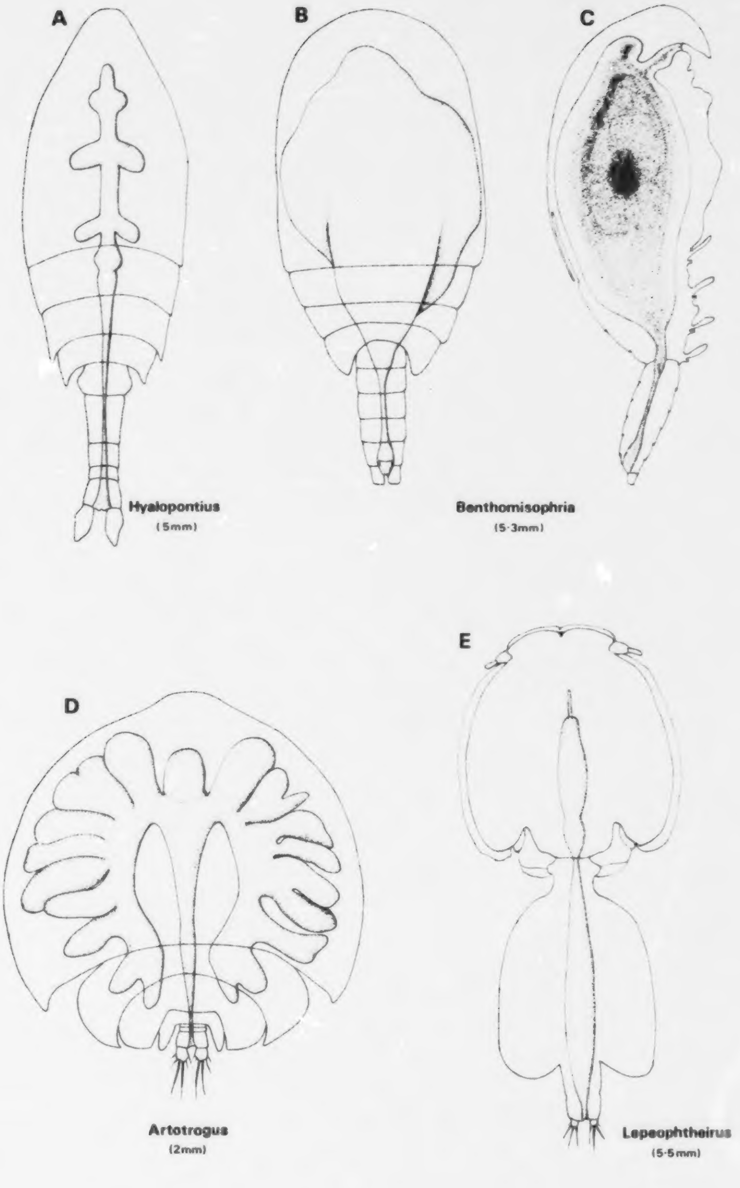
A
B
C
Hyalopontius
(5mm)
Benthomisophria
(5·3mm)
E
D
Artotrogus
(2mm)
Lepeophtheirus
(5·5mm)

Figure 5. *Gross morphology of the digestive tract of H. typicus* (**A**), *B. palliata dorsal* (**B**) *and in longitudinal section* (**C**), *Artotrogus orbicularis Boeck* (**D**) *and L. pectoralis* (**E**).

applied to the surface of their prey will create a good seal allowing them to suck up body fluids through the lesion made by their piercing mandibles. In *Lepeophtheirus* the oral cone opening is only partially surrounded by membranes on the labrum and labium and it feeds on pieces of host epidermis detached by the action of the labial strigil and raked into the oral cone by the mandibles (Kabata, 1974). Such pieces of tissue must be further fragmented before they can pass through the oesophagus. The ridged inner walls of the buccal cavity may act as a gizzard accomplishing this mechanically or the secretions released into the buccal cavity by the labral glands may have a pre-ingestion digestive function.

In marked contrast the nerve ring of *Benthomisophria* has a large diameter allowing considerable dilation of the oesophagus for the passage of large food items. *Euaugaptilus* has a similar ability to ingest large particles, as also do the predatory cyclopoids (Fryer, 1957).

Differences in feeding strategy are also reflected in the gross morphology of the midgut which in most copepods is a straight tubular structure extending from the oesophagus through to the posterior part of the urosome where it is separated from the hind gut by a valve. Most copepods have a small anterior midgut caecum extending forwards from the level at which the oesophagus enters the midgut. It is well developed in gorging forms, such as *Benthomisophria*, and in predators, such as *Euaugaptilus*, in which it acts as a storage area. Its volume is insufficient for storage in the gorging *Benthomisophria* and in this form the whole anterior part of the midgut is capable of gross distension (Figures 5b and c). The lateral expansion of the midgut can be regarded as lateral caeca which provide sufficient storage for *Benthomisophria* to take advantage of any rare opportunity for a large meal in its deep sea habitat.

Paired lateral caeca are also found in siphonostomes. Typically only one pair is present although these may be multilobed and can occupy a large volume of the prosome, as in *Artotrogus* Boeck (Figure 5d). *Hyalopontius* is unusual in possessing three pairs of lateral caeca (Figure 5a). The presence of lateral caeca has traditionally been explained as an adaption to a parasitic mode of life, as in the Branchiura. However, true parasites such as *Lernaeocera* de Blainville, members of the Lernaeopodidae and *Lepeophtheirus* (Figure 5e) have a narrow tubular midgut lacking lateral caeca. In these forms which live permanently on their hosts a large storage capacity is unnecessary as food is constantly available. It seems probable that forms with large lateral caeca, such as *Artotrogus*, are only temporarily associated with their hosts/prey, or at least only feed intermittently. These forms are frequently taken free in plankton or dredge samples rather than attached to a host and it is possible that they behave like micropredators, attaching to a prey temporarily whilst feeding, then dropping off again.

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PANEL DISCUSSION: COPEPOD PHYLOGHENY

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The discussion consisted of two parts: (1) presentation of their views on the phylogeny of individual groups of Copepoda by panel members, and (2) discussion proper by the panellists and participants from the floor. The initial presentations were as follows:

Dr. G.A. Bosxshall	(Siphonostomatoida and Mormonilloida)
Dr. Ju-shey Ho	(Cyclopoida)
Dr. J.H. Stock	(Poecilostomatoida)
Dr. B.M. Marcotte	(Harpacticoida)
Dr. Taisoo Park	(Calanoida)

The discussion proper was prepared by the moderator from the tapes recorded during the session.

PHYLOGENY OF MORMONILLOIDA AND SIPHONOSTOMATOIDA

G.A. BOXSHALL

Department of Zoology, British Museum (Natural History), London SW7 5BD, England

MORMONILLOIDA

The Mormonilloida are rarely seen except by those working in the deep mesopelagic. This order comprises one genus with 2 species, both reasonably abundant in the Atlantic Ocean, at least, between 400 and 1000 m. Their distribution extends through all the major ocean systems and vertically down to over 4000 m. I will be talking about their feeding biology in the behaviour symposium but what is striking about Mormonilla is the relatively large size of its filter apparatus. This occupies the anterior third of the body. The filter apparatus comprises the palps of the mandible and maxillule and the exopod of the antenna lies on top of these. The antennary endopod lies external to the endopodal setae of the palps closing off this filter basket midventrally. The maxilla and maxilliped have a different kind of basal articulation and move around within the space enclosed by the basket of plumose setae. This filter basket is closed off posteriorly by the first swimming legs.

The important characters of the Mormonilloida include:

1. A 3- or 4-segmented antennule. Reduction of numbers of antennule segments is a very common trend in all copepod orders and it is highly reduced in mormonilloids.
2. Exopod of antenna 8-segmented.
3. Biramous mandibular palp, but rami partially incorporated into the basis.
4. The first legs appear to be involved in the feeding process forming a posterior barrier for the filter basket. They have unusually strong spinous processes along the inner surface of the endopod and a peculiar sigmoid seta with denticles. I interpret these as a means of preventing food loss from the filter basket via the median space between the legs.
5. They have no leg 5, at least in the adult, and the developmental stages are completely unknown as far as I am aware.
6. Their tagmosis is typically podoplean. The urosome is only 4-segmented as they possess a genital complex formed by the fusion of the genital somite and the first abdominal somite.

I am at present unable to understand the reproductive biology of this genus. Both M. phasma and M. minor are known only from females, no males or females with egg sacs or carrying spermatophores have ever been reported in the literature. From serial sections and whole mounts I have reconstructed the gross morphology of the reproductive system. It comprises paired gonads (ovaries) and ducts which open via a single median ventral genital aperture, rather like in calanoids. However, what I interpret as developing ova are present in the gonad of the same individual, which appears to have a chitinous spermatophore lying distally in the duct awaiting extrusion. So I don't really understand the reproductive biology of this species.

I have found one female in over 2000 m that I have looked at which had a spermatophore attached.

It is possible that it is the spermatophore of a rampant male of an entirely different copepod species but what is interesting about it is that it was not attached near the median genital aperture. The neck of the spermatophore disappeared into a small pore lateral to the genital aperture. This pore was in communication with the chamber (genital antrum or vulva) beneath the genital aperture. I do not want to place too much emphasis on a single specimen but this separation of the incoming male pore (through which the spermatophore discharges) from the main genital aperture through which eggs are released would be a unique character. This animal is really quite common and needs more study.

SIPHONOSTOMATOIDA

The Siphonostomatoida is a large order containing 1400 to 1500 species in about 40 families (Table 1). The list is basically as contained in Bowman and Abele (1982) although I have omitted the Catlaphilidae because I believe this represents a damaged Lamproglena (Lernaeidae). The Nicothoidae incorporates the Choniostomatidae. These are listed according to the classic division into those parasitising fishes and those parasitising invertebrates or with no known host but which are assumed to parasitise invertebrates because they are cyclopiform in shape and resemble others in this category. Until Kabata's monograph (1979) the siphonostome parasites of invertebrates were generally classified as the Cyclopoida Siphonostoma and the siphonostome fish parasites were arranged in two orders, the Caligoida and Lernaeopodoida. All are now united within the Siphonostomatoida and they form a cohesive group defined by the possession of a stylet-like mandibular gnathobase typically contained within an oral cone formed by the labrum and the labium.

I will show you 4 examples (a eudactylinid, lernaeopod, nicothoid and an etomolepid) to give you an idea of the potential and diversity of the group.

I have chosen one relatively unmodified example to examine in more detail the characters of the group. It is Hyalopontius enormis, the largest planktonic siphonostomatoid at 7.5 mm long but is free swimming in the bathypelagic environment. The characters of the group can be seen:

1. Relatively large numbers of antennule segments, up to 21 in the Asterocheridae
2. Bilaterally geniculate antennules in the male
3. 1-segmented exopod on antenna or exopod absent. There is some indication of 2 segments in a species of Dermatomyzon figured by Giesbrecht (1899).
4. Mandibular gnathobase stylet-like, extending down the oral cone; palp reduced to a single ramus or lost.
5. Bilobed maxillule, generally referred to as inner and outer lobes although Giesbrecht (1899) called inner lobe the gnathobase and outer lobe the palp.
6. Maxilla subchelate with claw formed from endite on basis.
7. Maxilliped subchelate with claw formed from segments of ramus and basis.
8. Leg 5 lacks any vestige of an endopod.
9. They possess a genital complex from the fused genital somite and the first abdominal somite.

That just about completes my introduction to this group but for one problem. Marcotte (1982) suggested the possibility of a polyphyletic origin of the Siphonostomatoida and others here have voiced the same opinion. So, I thought it would be appropriate for me to address this problem briefly at this discussion.

Table 1. *Families of SIPHONOSTOMATOIDA*

FAMILIES	GENERA	SPP	FAMILIES	GERNERA	Spp
Megapontiidae	1	8	Dissonidae	1	8
			Trebiidae	2	14
Pontoeciellidae	1	1	Caligidae	23	350+
			Pandaridae	12	36
Rataniidae	1	2	Euryphoridae	5	23
			Cecropidae	5	6
Asterocheridae	28	98			
Dinopontiidae	2	3			
Artotrogidae	10	55			
Myzopontiidae	3	6	Eudactylinidae	6	38
Dyspontiidae	4	8			
Entomolepidae	4	6	Dichelesthiidae	2	2
Nanaspidae	3	16			
Stellicomitidae	5	11	Kroyeridae	2	18
Micropontiidae	1	2	Pseudocycnidae	2	4
Cancerillidae	6	11	Hatschekiidae	5	76
			Lernanthropidae	5	120+
Brychiopontiidae	1	2	Hyponeoidae	1	1
Calvocheridae	1	3	Pennellidae	18	120
Thespesiopsyllidae	2	2	Lernaeopodidae	36	185+
			Naobranchiidae	1	19
Dirivultidae	2	2	Tanypleuridae	1	1
			Sphyriidae	7	21
Spongiocnizontidae	1	3			
Nicothoidae	17	110			
Saccopsidae	1	4			
Herpyllobiidae	4	17			
Xenocoelomidae	2	2			
'Family unknown'	11	19			
Total parasitic on invertebrates	111	388	Total parasitic on vertebrates	134	1042+

Totals for order Siphonostomatoida:
Families = 40
Genera = 245
Species = 1430+

The taxon Siphonostomatoida is defined on the possession of a mandible reduced to a stylet-like gnathobase with or without a uniramous palp and an oral cone formed by the anterior labrum and posterior labium. Re-examining the diagnosis let me ask 'what exactly is the labium?' Within the copepods only the siphonostomes primitively possess one. The labial musculature indicates that the labium is derived by the medial fusion of the paired paragnaths. In the calanoid Euaugaptilus the paragnaths are ridge like, highly chitinised structures but in other copepods such as some Cyclops species, as described by Fryer (1957), the paragnaths can be adducted by a curious indirect mechanism. The paragnath adductor muscles originate on the ventral surface of the anterior ventral cephalic tendon. They pass through channels in the suboesophageal ganglion before inserting on the paragnaths. In Hyalopontius the labial muscles have precisely the same site of origin, on the single cephalic tendon, and course through the ganglion before inserting. It seems clear that the labium represents fused paragnaths. I consider that this provides evidence of a shared derived homologous character state linking all siphonostomes but there is even more convincing data when we look at the muscles that move the oral one.

Some siphonostomes are able to move their oral cone to raise it perpendicular to the body surface. The caligids are good examples of this but the planktonic cyclopiform type Pontoeciella, from the 'invertebrate host category' also has a moveable oral cone. Erection of the oral cone is accomplished by two pairs of levator muscles. In Lepeophtheirus they originate on the postmaxillulary apodeme, pass anteriorly through the nerve ring and insert on the buccal apodemes at the base of the oral cone. As they pass through the nerve ring they present a distinctive configuration in transverse section. When I examined sections of Pontoeciella I found precisely the same configuration of four levator muscles passing through the nerve ring and having the same origin and insertion sites. In my opinion, this constitutes a synapomorphy linking siphonostomes from the two host categories together as advanced siphonostomes.

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PHYLOGENY OF CYCLOPOIDA

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The cladistic analysis is an useful method for reconstruction of evolutionary history. It became popular among the systematists only in the last 10 to 15 years. Since this method is seldom used by the copepodologists, I take this opportunity of presenting the phylogeny of Cyclopoida to demonstrate the applicability of this method to the study of Copepoda. Due to a limited time for preparing this presentation, only the cephalosomal appendages were taken into consideration.

FAMILIES OF CYCLOPOIDA

Kabata (1979) has adequately redefined the scope of the Cyclopoida and Bowman and Abele (1982) recognized 14 families in this order. However, according to Illg and Dudley's (1980) work on the copepod parasites of ascidians, five of these 14 cyclopoid families (Botryllophyllidae, Buproridae, Enterocolidae, Enteropsidae, and Schizoproctidae) should be relegated to the subfamilial rank of the Ascidicolidae. Furthermore, Doropygidae has long been considered a synonym of the Notodelphyidae (Illg, 1958) and Namakosiramiidae should have been placed in the Order Harpacticoida. Namakosiramia californiensis is the sole member of the latter family, it has, based on Ho and Perkins' (1977) description of this species, some typical harpacticoid features, like: (1) a rudimentary exopod in the second antenna, (2) the oviducal openings on the ventral surface of the genital segment, and (3) a prehensile first pair of legs.

With the removal of these seven families, the Order Cyclopoida is now left with seven families, namely Archinotodelphyidae, Ascidicolidae, Cyclopidae, Cyclopinidae, Lernaeidae, Notodelphyidae, and Oithonidae. This order is an assemblage of free-living and parasitic copepods, with about 500 species occurring in both freshwater and marine habitats.

The Cyclopidae (Figure 1) is largely freshwater, with a few species occurring in brackish water or littoral zone of the ocean. The Cyclopinidae (Figure 1) assume a body form similar to the Cyclopidae and they live predominantly in coastal waters. However, the Oithonidae (Figure 1) are different, they possess a streamlined body and are found in both coastal and oceanic waters. While these three families are free-living, the remaining four families are parasitic.

The Archinotodelphyidae (Figure 1) is the smallest family of the Cyclopoida, consisting of only 5 species (in 3 genera). They are also the least modified parasitic cyclopoids, retaining a great deal of podoplean tagmosis and body segmentation. They are found in the tunicates and marine bivalves. The notodelphyids (Figure 2) are parasitic in the ascidians. The females are unique in carrying their eggs inside an incubatory chamber. Some of them are so highly modified that they can hardly be recognized as copepods. Members of the Ascidicolidae (Figure 2) are largely parasitic in the ascidians, but those of

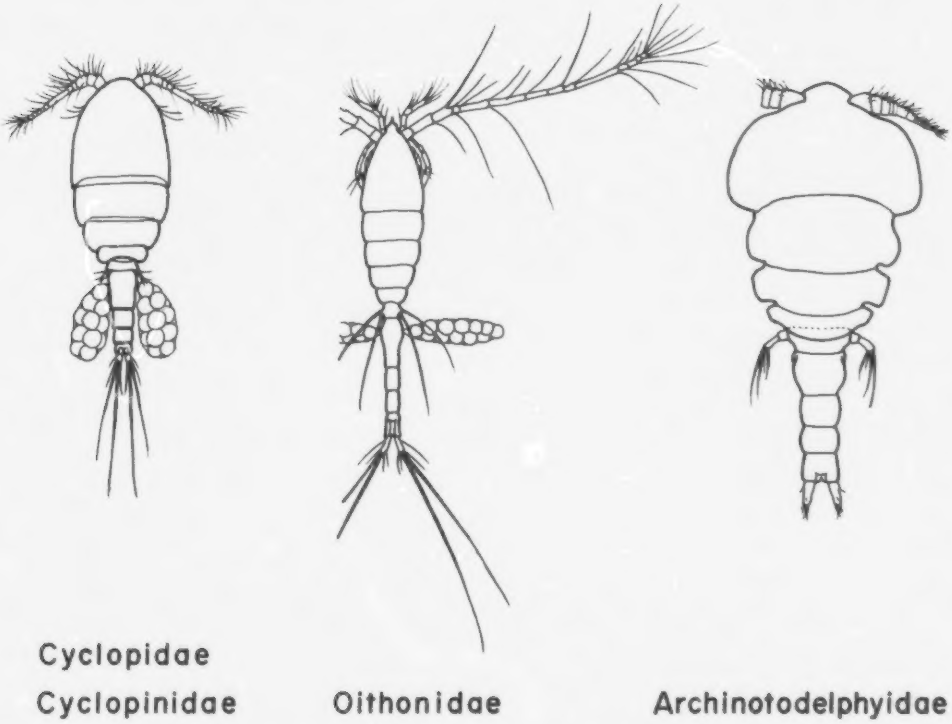

Cyclopidae
Cyclopinidae
Oithonidae
Archinotodelphyidae

Figure 1. *General body forms of free-living and less modified parasitic cyclopoids*

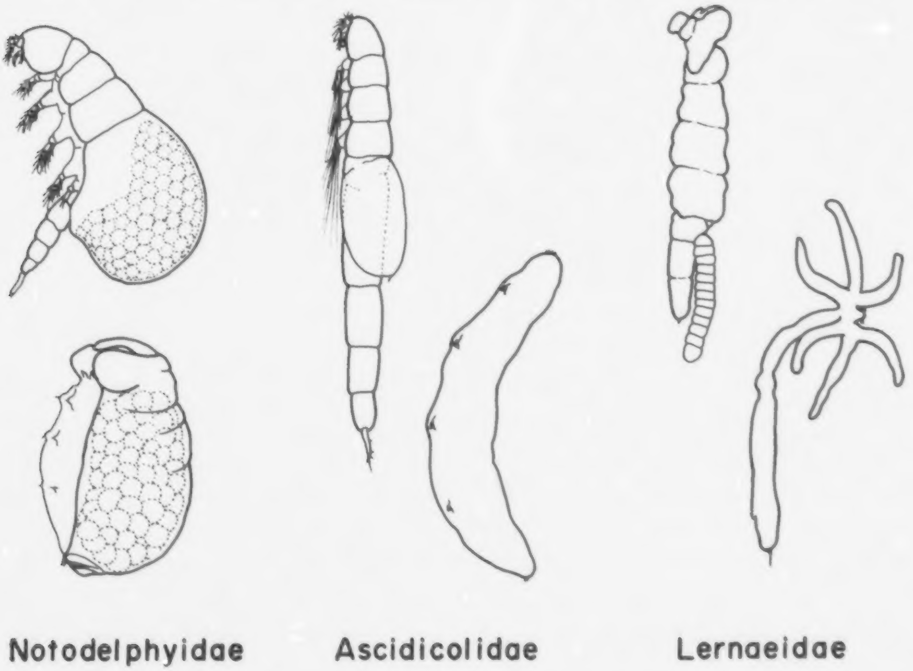

Notodelphyidae
Ascidicolidae
Lernaeidae

Figure 2. *General body forms of parasitic cyclopoids. Showing in each family a less modified and a highly modified form.*

the Lernaeidae (Figure 2) are parasites of freshwater fish. Many members of the last two families are also very highly modified.

CHARACTER ANALYSIS AND CONSTRUCTION OF CLADOGRAM

The character analysis is a vital process in conducting the cladistic analysis. It is a process to determine the evolutionary states of all selected characters. Each character in a given taxon (excluding species) may have only one state of transformation. If a character has multiple states of transformation, it becomes a problem to decide which state should be selected to represent the character of the taxon in question. The common practice in this case is to select the most primitive state, because this state is assumed to represent (or to be closest to) the ancestral state of the given character for the given taxon. For instance, in the Cyclopidae, the number of segments on the first antenna ranges from 6 (in Clocyclops) to 21 (in Eurete) and the prevalent view of this character is: the higher the number the more primitve is the state; then, the character state of the first antenna for this family is to be set at 21 segments.

Another purpose of conducting character analysis is to determine whether the assigned state of a character is in plesiomorphic (primitive) or apomorphic (derived) state. To make this decision, we need to examine the ontogenetic development of the character in question and/or to compare it with the homologue found in the outgroup. Since ontogenetic information is not always available, the outgroup comparison is more frequently used. An outgroup should be closely related to and generally more primitive than the taxon under consideration. The Order Misophrioida is generally considered representing a group of primitve podopleans. Therefore, it is selected to serve as the outgroup for determining the polarity of the character states in the Cyclopoida. For instance, the misophrioids have a well-developed exopod in their second antennae, but this exopod is absent in all the cyclopoids; therefore, the uniramous second antenna in the cyclopoids are considered to be in an apomorphic state. The 3-segmented second antenna in the Ascidicolidae, Lernaeidae, and Notodelphyidae is another derived feature, because the plesiomorphic state exhibited in the misophrioids is a 4-segmented structure. One more derived state in the cyclopoid second antenna is recognized, it is the possession of a terminal claw. The development of this claw, the missing of the exopod, and the reduction of the segments are deemed to be independent events that occurred in the course of the cyclopoid evolution. Hence, there are three separate series of character transformation in the cyclopoid second antenna.

Most families of Cyclopoida have a rather conservative mandible (Figure 3), with a masticatory lamella (gnathobase) and a well-developed biramous palp bearing a 4-segmented exopod and a 2-segmented endopod. The structure of the palp shows a great deal of interfamilial variation. For instance, in the Ascidicolidae it is a biramous structure with 1-segmented endopod and 2-segmented exopod, in the Cyclopidae it is reduced to 3 setae, and in the Lernaeidae it is entirely lost. These various states of the mandibular palp is an example of complex transformation (vs. the linear transformation that is represented by the cyclopoid first antenna) with their states transformed in a radiating pattern as shown in the following:

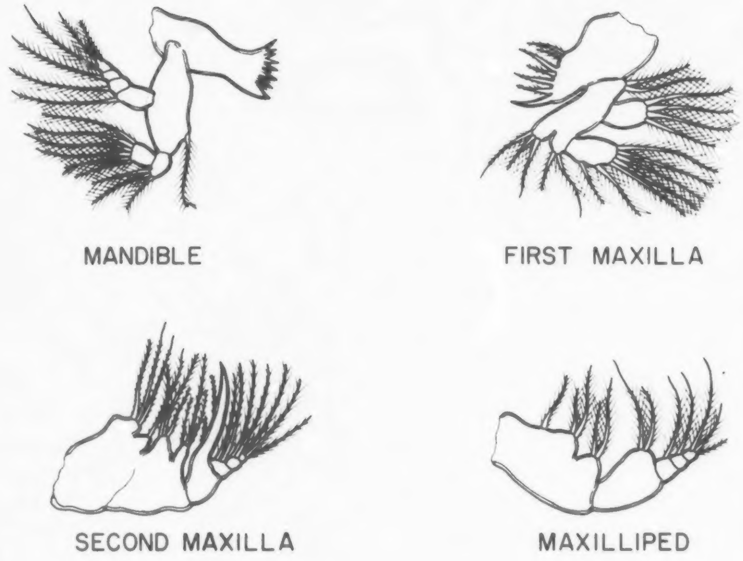

MANDIBLE
FIRST MAXILLA
SECOND MAXILLA
MAXILLIPED

Figure 3. *Plesiomorphic states of cyclopoid oral appendages.*

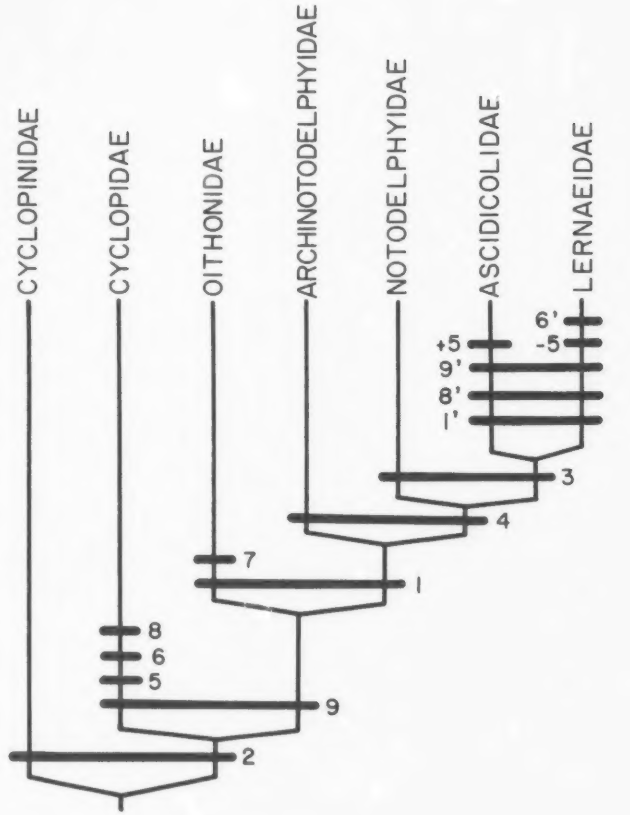
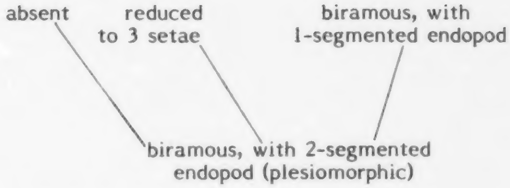

CYCLOPINIDAE
CYCLOPIDAE
OITHONIDAE
ARCHINOTODELPHYIDAE
NOTODELPHYIDAE
ASCIDICOLIDAE
LERNAEIDAE
6'
-5
+5
9'
8'
1'
3
4
7
1
8
6
5
9
2

Figure 4. *Cladogram of Cyclopoida. See Table 1 for character codes.*


absent
reduced to 3 setae
biramous, with 1-segmented endopod
biramous, with 2-segmented endopod (plesiomorphic)

The transformation in the cyclopoid first maxilla (Figure 3) is about the same as in the mandible, with most of the changes occurring in the palp (including the basis and the rami). The Cyclopidae have reduced certain parts of the rami and the basis but the Lernaeidae have lost them entirely. Both Notodelphyidae and Ascidicolidae show a great deal of intrafamilial variation in the structure of the rami but, otherwise, their plesiomorphic states are not much different from the Archinotodelphyidae, Cyclopinidae, or Oithonidae.

The ancestral second maxilla (Figure 3) in the Cyclopoida is characteristic in having the inner surface of the basis drawn out into a large pointed hook and bearing distally to it a small 3-segmented endopod. Two different series of transformation are observed: one involves reduction of the hook, which is represented by the Oithonidae, and the other one, the reduction of the endopod, which is represented by the Cyclopidae. The second maxilla of the Ascidicolidae and Lernaeidae exhibits a state of further reduction from that of the Cyclopidae, the endopod missing entirely and the coxa and basis are fused into one piece.

The ancestral state of the cyclopoid maxilliped (Figure 3) is retained only by the Cyclopinidae, with a small endopod bearing three segments. This 3-segmented endopod is reduced to a 2-segmented structure in the Cyclopidae, Oithonidae, Archinotodelphyidae, and the Notodelphyidae, and absent in the Ascidicolidae and Lernaeidae.

The various character states discussed above are summarized in Table 1, where each character or each transformation series of a character is coded with a number from 1 to 9. Of the six pairs of cephalosomal appendages, the second antenna has three series of transformation, the second maxilla has two, and each of the remaining four appendages has only one series.

Based on the coding system given in Table 1, the character states of the seven cyclopoid families are transcribed into a series of codes as shown in Table 2. This table, which is called a data matrix, is then used to construct the cladogram. I employed a method called Quantitative Parsimony Analysis (Brooks, 1984) to construct the cladogram.

EVOLUTIONARY HISTORY

Several cladograms can be produced from a data matrix, but only the most parsimonious one (showing the maximum congruence) is taken into consideration in the analysis of phylogeny.

As shown in Figure 4, the most parsimonious cladogram of the Cyclopoida indicates that the unifying character of this order is the lack of an exopod in the second antenna. In other words, the common ancestor of the misophrioids and cyclopoids lost the exopod on the second antenna and evolved into the copepods of the Cyclopoida. The Cyclopinidae is the group closest to the ancestral form, without developing apomorphic characters in the cephalosomal appendages. It is interesting to note that

Table 1. *Cephalosomal appendages and their states used in the cladistic analysis.*

Character	Code	Plesiomorphic	Apomorphic
First antenna	1	0 : 21 to 26 segments	1 : 15 to 17 segments
			1': 6 or 7 segments
Second antenna	2	0 : bearing an exopod	1 : without exopod
	3	0 : uniramous, with 4 segments	1 : uniramous with 3 segments
	4	0 : without a claw	1 : tipped with a claw
Mandible	5	0 : palp biramous,with 2-segmented endopod	-1 : palp missing
			1 : palp reduced to 3 setae
			+1 : palp biramous, with 1-segmented endopod
First maxilla	6	0 : palp biramous	1 : palp a setiferous lobe
			1': palp missing
Second maxilla	7	0 : basis with a claw	1 : basis without a claw
	8	0 : endopod 3-segmented	1 : endopod 1-segmented
			1': endopod missing
Maxilliped	9	0 : endopod 3-segmented	1 : endopod 2-segmented
			1': endopod missing

Table 2. *Basic data matrix of nine characters and their states used in construction of the cladogram.*

Taxa	Characters								
	1	2	3	4	5	6	7	8	9
Archinotodelphyidae (3)	1	1	0	1	0	0	0	0	1
Ascidicolidae (17)	1'	1	1	1	+1	0	0	1'	1'
Cyclopidae (34)	0	1	0	0	1	1	0	1	1
Cyclopinidae (21)	0	1	0	0	0	0	0	0	0
Lernaeidae (10)	1'	1	1	1	-1	1'	0	1'	1'
Notodelphyidae (45)	1	1	1	1	0	0	0	0	1
Oithonidae (4)	1	1	0	0	0	0	1	0	1

Note: Numbers in parentheses indicate the number of genera and subgenera.

the four parasitic families are allied in a cluster which is separated from the free-living families by one synapomorphy(shared derived character) - possession of a terminal claw in the second antenna. This synapomorphy can also be interpreted that the development of a prehensile second antenna is an evolutionary novelty that enabled the cyclopoids to explore a mode of life other than the free-living.

The Cyclopidae show more changes in the mouth parts than the Oithonidae, another free-living family. The evolutionary changes that occurred in the mandible, first maxilla, and second maxilla had led the cyclopoids into a possible shifting of food habits. They no longer feed on plankton, instead, they are either carnivorous (feeding on chironomid larvae, oligochaetes, fish larvae, etc.) or herbivorous (feeding on algae and plants). Although oithonids retain the ancestral feeding habit (filter feeding), a majority of them have moved out of the ancestral habitat, from coastal to oceanic waters. This successful shift of habitat is considered to be made possible through the change that occurred in the second maxilla. In the Oithonidae this appendage is drawn out and lacks a hook on the basis, it is a much efficient apparatus for filtering food in oceanic waters.

The freshwater copepods are supposed to have evolved from the marine forms. In the case of the Cyclopoida, it seems that they have invaded the freshwater regime twice at two different stages of their evolution. The first invasion took place before the development of a terminal claw in the second antenna and the second invasion took place after the cyclopoids had developed this claw (see Figure 4). The first invasion, that was made by the free-living forms, resulted in the development of the Cyclopidae and the second invasion, led by the parasitic forms, gave rise to the Lernaeidae. This inference from the cladogram is quite different from the prevalent view that the freshwater fish parasitizing Lernaeidae had evolved from the freshwater free-living Cyclopidae.

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PHYLOGENY OF POECILOSTOMATOIDA

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The boundary between the Cyclopoida and the Poecilostomatoida is slight in comparison with that between other copepod groups. Especially between the genus Halicyclops (Cyclopoida) and Hemicyclops (Poecilostomatoida), the only fundamental morphological differences appear to be the presence of geniculate anterior antennae (an apomorphic character) in the former. The ecological difference between the Cyclopoida (in overwhelming majority free-living) and the Poecilostomatoida (almost entirely associated with or parasitic on invertebrates and fishes) is also obscured by the two genera just-mentioned: certain species of Halicyclops show tendencies towards association with marine polychaetes of the genus Nereis (Herbst, 1962), several species of Hemicyclops appear to be free-living, interstitial (Gooding, 1963).

Starting from the basic group of the poecilostomes, the family Clausidiidae, two discrete lines of evolution can be observed. The characters separating these lines are by no means absolute, exceptions not being rare, especially among the more apomorphous, transformed, taxa of parasites. One might prefer to speak of "tendencies" instead of "lines". The two lines in question are:

1. Myicolidae - Clausidiidae - Synaptiphilidae - Nereicolidae, etc.
   - Accentuation in size and function of P5, the distal segment of which is armed with at least 4 (rarely 3) elements.
   - Mandible specialized (elaborate ornamentation, and/or with several lashes).
   - Modification of A2 towards strongly prehensile organs (strong claws, suckers).
   - Gradual reduction of number of segments in A1, starting from the basic number of seven.
   - Maxilliped often modified into strongly prehensile organs, also in the female sex.
   - Reduction of the number of urosomites (basically 5 in ♀, 6 in ♂).
   - Fusion of metasomites (basically 3).
   - Frequent reductions in the biramous legs in a series posterior to anterior.
2. Sabelliphilidae - Lichomolgidae - Pseudanthessidae - Rhynchomolgidae.
   - P5 in (strong) reduction, usually armed with 2 elements only.
   - Mandible simplified (not elaborately armed, only 1 lash).
   - A2 feebly prehensile (many exceptions are known, however).
   - A1 retaining 7 segments.
   - Maxilliped (♀) in reduction, loosing prehensile function.
   - Number of urosomites usually basic (5 in ♀, 6 in ♂).
   - Metasomites usually not fused.

- Sometimes reductions in the biramous legs; if reduced, both a posterior-anterior or an anterior-posterior series may occur.

Difficulties arise mainly with the location of the fish parasites. The two lines mentioned above contain almost exclusively associates of invertebrates, but some notable exceptions may prove to be significant: Avdeev et coll. (in press) have discovered fish parasites that clearly belong to the Myicolidae, a family mainly associated with marine mollusks. The second case concerns the family Taeniacanthidae, a family of fish parasites, with a few representatives found on echinoids. These two facts suggest that there is gradual transition of the associates of invertebrates into the parasites of fishes. As a point of fact, several more plesiomorphous families of fish parasites (Bomolochidae, Taeniacanthidae) seem to fit better in the myicolid/clausiid line than in the lichomolgid line, as shown by the morphology of their P5, A2, and the mandible.

The more apomorphous fish parasites have so strongly modified (or transformed) bodies and appendages, that allocation to any of the two lines is virtually impossible. If the ecology (i.e., parasitic on fish) is counted heavily, it sounds logical to assume a monophyletic origin of all these forms and to derive these fish parasites (Chondracanthidae, Philichthyidae....) likewise from myicolid clausiid ancestors. The mandibular structure does not prevent such an assumption. However, it must be borne in mind that not all fish parasites are of monophyletic origin, but that they are derived from Cyclopoida, Poecilostomatoida, and Siphonostomatoida. A study on larval stages may solve perhaps the question of the evolutionary origin of the poecilostomatoid fish parasites.

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PHYLOGENY OF THE COPEPODA HARPACTICOIDA

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Various aspects of copepod morphology, e.g. juvenile and adult body divisions, the morphologies of oral and locomotory limbs and the presence of a nauplius larva, may have evolved independently in several crustacean groups including the extant Remipedia Yager, 1981, the Branchiopoda Lipostraca Scourfield, 1926 and Tesnusocaris Brooks, 1955. Nevertheless, because animals which look the same must be assumed to be phylogenetically related until proven otherwise (Hessler, 1982), the subclass Copepoda will be assumed to be a monophyletic assemblage for the purposes of this essay.

Neoteny of a crustacean ancestor, such as Lepidocaris Scourfield, 1926, has been assumed to be a likely morphological mechanism for the origin of the Copepoda and the Maxillopoda generally (e.g. Garstang and Gurney, 1938; Boxshall, 1983; Newman, 1983; see also review in Marcotte, in press). A phylogeny which aspires to be more than a series of "just so" stories must include an account not only of the morphological mechanism for a taxon's origin but some reason for its selective advantage and thus for its persistance and diversification. Three such reasons can be offered for a neotenous origin of the Copepoda: 1) a selective advantage to staying young and, therefore, small to avoid competition for food (Marcotte, 1977, 1983), 2) the hydrodynamic benefits for foraging efficiencies, in a turbulent and potentially turbid medium, of being small and fast moving (Purcell, 1977; Alcaraz et al. 1980; Koehl and Strickler, 1981; Strickler, 1982, in press; Price et al. 1983; Marcotte, 1983, in press), and 3) life history adaptations to increasing frequencies and decreasing durations of environmental perturbations (Marcotte, in press). These causes for the selection of neotenous taxa can be used to estimate a geological time for the origin and/or diversification of the copepods: Silurian-Devonian and/or Jurassic-Cretaceous (Marcotte, in press). The existence of Lepidocaris in Devonian habitats supports an early origin for the Copepoda.

Whatever the timing of the origin of the Copepoda, a benthic or epibenthic ancestor is likely (Marcotte, 1982; Figure 1). This animal would have been slow-moving and would have foraged in the viscosity-dominated water layers at the sediment-seawater interface where chemical gradients produced by food organisms diffuse in predictable trajectories across the bottom. These gradients would have been used to efficiently locate patches of food (Marcotte, 1977, 1983, in press). The harpacticoid Tisbe is probably similar to this ancestor but Tisbe itself is probably too derived to be the actual ancestor (Marcotte, 1977).

From this ancestor other copepod taxa gradually evolved (Figure 1) through responses to new environments, exploration of which was initiated by changes in swimming, feeding, mating or other behaviours (e.g. Marcotte, 1984). The first of these changes may have been caused by competition for space and led to the evolution of natant harpacticoids e.g. Longipediidae, Canuellidae, and, eventually some ectinosomatids. This line of swimming taxa, eventually led to the near-bottom Misophrioida and, ultimately, to the anatomically specialized Calanoida, with hydrodynamically smooth bodies, anatomically linked locomotory legs and high-speed foraging mechanisms and to the enigmatic Mormonilloida. It is interesting to note that epiphytic, epibenthic, demersal planktonic, and planktonic copepods represent steps along a continuous gradient of morphometric transformation in which the prosome was laterally compressed while the urosome remained relatively constant in breadth and length (Figure 2). This conservative feature of urosome evolution may have been the result of complicated mating biologies in which the urosome of both males and females must be changed simultaneously and in which copulation in water placed constraints on the choreographies which involved the urosome permitting successful transfer of spermatophores. Discontinuities in this morphometric gradient occurred as inbenthic and parasitic forms evolved (Marcotte, 1980).

With the origin of inbenthic taxa, a major adaptive radiation of copepods began (Figure 1). The first of these forms were probably like the present day Ectinosomatidae, harpacticoids which swim at the sediment-seawater interface and dart into the first millimeters of the sediment to forage and, with some, to escape predators. These animals have robust exoskeletons which are hydrodynamically smooth and strong enough to withstand frequent collisions with sediment. The locomotory legs of these ectinosomatids are usually biramous and each ramus is usually tri-articulate, long and broad. When they are used to propel the animal through the water, they are fully extended. As the animal enters the

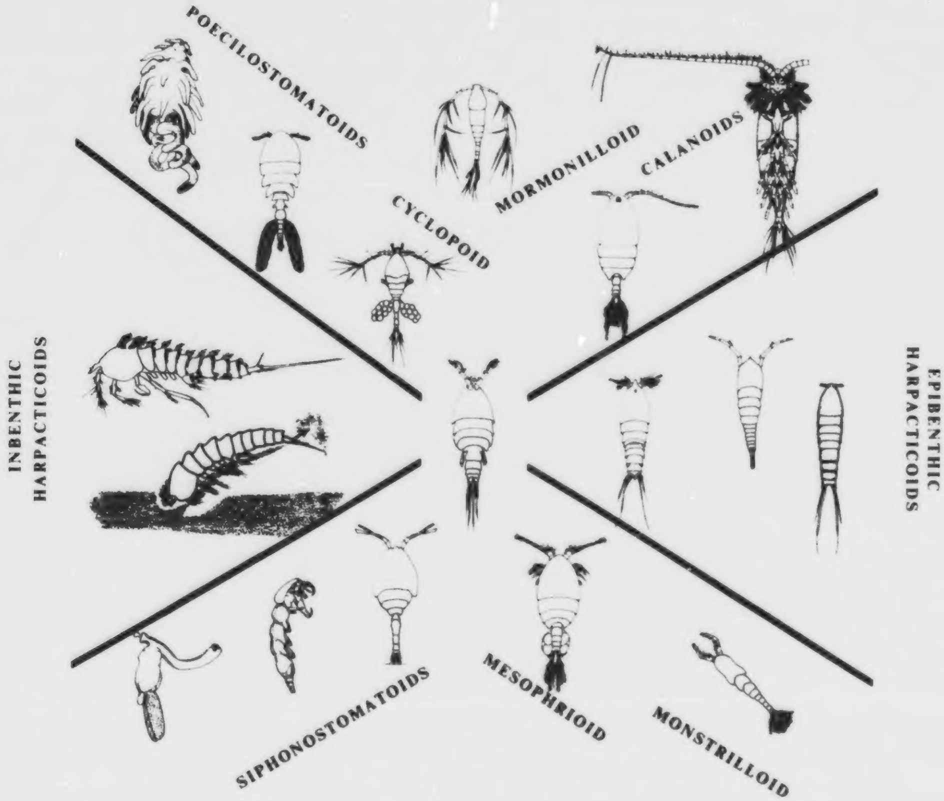

Figure 1. *Major lineages of the Copepoda radiating from the epibenthic harpacticoid* Tisbe *(center). Ancestral taxa of major lineages are pictured closest to the centre.*

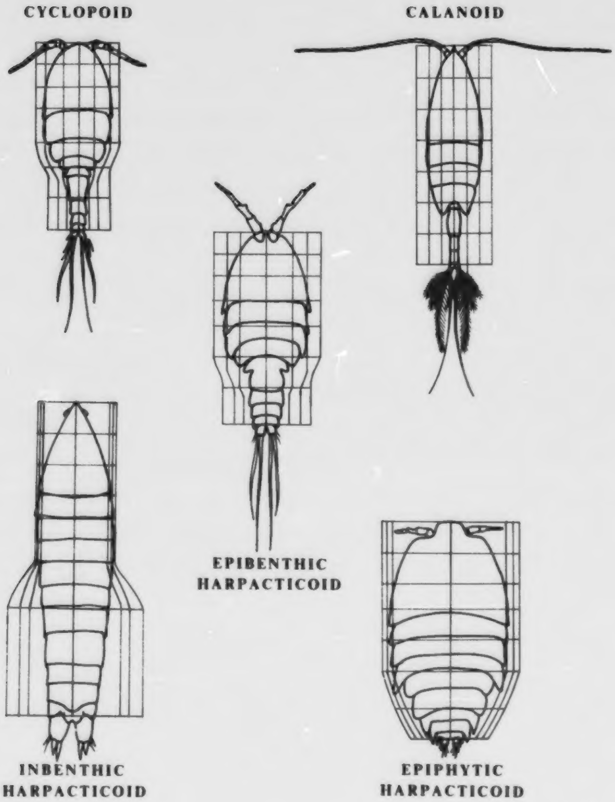
CYCLOPOID
CALANOID
EPIBENTHIC HARPACTICOID
INBENTHIC HARPACTICOID
EPIPHYTIC HARPACTICOID

Figure 2. *Morphometric transformations among major free-living copepod taxa. The morphometric changes with the evolution of the inbenthic harpacticoids (here illustrated with* *__Halectinosoma__*) *are discontinuous with all other transformations illustrated.*

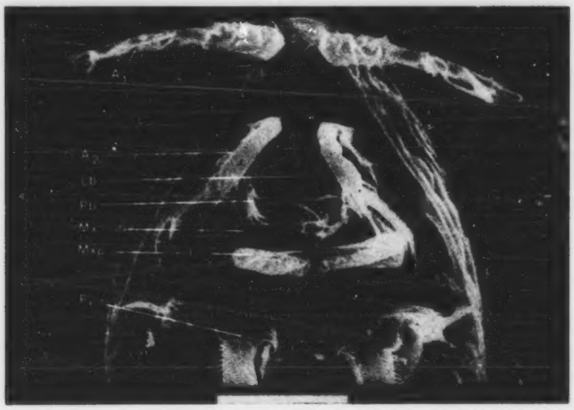
A_1
A_2
Lb
Pb
Mx
Mxp
P_1

Figure 3. *Scanning electron micrograph of the mouth parts of* *__Tisbe__* *sp.. A1 = first antenna, A2 = second antenna, Lb = labrum, Pb = palp of the mandible, Mx = claw of the second maxilla, Mxp = maxilliped, P1 = first locomotory limb. White bar at centre-bottom is 100 um long. Photograph curtesy of C. Bradford, Calloway, Havard University.*

sediment, it laterally extends its caudal rami apparently to slow its movement and to direct its entry into the surface layer of the sediment. Upon entry into the sediment the animal's locomotory legs become bent ventrally and posteriorly from the distal end of the proximal article and the animal shuffles its way through the sediment as if on its knees. Cuticular spines on the ventral face of the legs are used to help purchase the sediment. Many of these early forms, represented today by the genera Halectinosoma and Pseudobradya forage for food by scraping micro-organisms non-selectively from the surface of particles of sand. In sandy habitats interstitial harpacticoids may have evolved from these first inbenthic forms through reduction in body size especially of body width in relation to length and through reduction in the number of rami, articles and ornamentations on locomotory legs. Many of these interstitial forms became very selective epistrate feeders (pers. obs.). Other inbenthic harpacticoids lived in muddy habitats and became specialized for feeding on micro-organisms living on particles present in these sediments which display a great diversity of geometric shapes. Anterior locomotory appendages are used to hold onto plants, sedimentary particles and perhaps prey. In some of the most advanced forms such as the Laophontidae, the first locomotory leg is transformed into a large maxilliped-like appendage (Figure 1). These animals are capable of moving mouth parts on either side of the body independently so that bilaterally asymmetrical pairings of trophic limbs can function to manipulate food bearing substrates and prey. Other groups, such as the Cletodidae, became small. Their bodies became flexible; they became miniature conveyer belts which propelled themselves through soft sediments by dragging fine particulate matter in front of them down across their oral appendages with their first antennae (Figure 1). Food was sorted from inert material as the sediment was shuffled posteriad with special posterior oral appendages and with the endopods of their locomotory limbs. Thus, an overall trend in the diversification of inbenthic harpacticoids was an independent evolution of trophic strategies which ancestrally treated food resources as fine-grained phenomena (sensu Levins, 1968; see also Marcotte, in press) with derived forms experiencing food as a coarse-grained resource either because of copepod miniaturization with respect to the spatial distribution of the food or because of selective foraging tactics.

A second discontinuity in copepod evolution occurred with the advent of parasitism. The harpacticoid Tisbe illustrates some of the trophic features expected of ancestral parasites. First, it is carnivorous (Marcotte, 1977). Tisbe is known to eat the fins off a juvenile fish immobilizing it and then eat the body as it rests on the bottom. Such a predator could have evolved into a form which took bites out of its prey but did not kill it. Thus parasitism can originate (Fryer, 1957). Such a scenario may have led to the origin of the Cyclopoida from a Tisbe-like ancestor. The parasitic Copepoda Poecilostomatoida may have evolved from a cyclopoid ancestor while the parasitic Siphonostomatoida probably evolved from a harpacticoid. The buccal structure of Tisbe presage the origin of the Siphonostomatoida (Figur 3). The labrum, mandible and first maxilla of Tisbe are elongated and project ventrally as a conical stucture which resembles the conical siphon of ancestral siphonostomatoids. Such an oral structure seems preadapted for piercing a host's skin and strong peristaltic contractions of the foregut, a phenomenon which can be observed in Tisbe (Marcotte, 1977), may have made sucking a host's body fluids possible.

Thus, from a benthic, probably harpacticoid, ancestor, all the other copepod taxa, benthic, pelagic and parasitic can be derived.

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PHYLOGENY OF CALANOID COPEPODS

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The order Calanoida is a rather homogeneous group adapted primarily to planktonic life and supposed to be a monophyletic group. Andronov (1974) divided the Calanoida into 9 superfamilies: Platycopioidea, Pseudocyclopoidea, Augaptiloidea, Centropagoidea, Megacalanoidea, Bathypontioidea, Eucalanoidea, Ryocalanoidea, and Pseudocalanoidea. Bowman and Abele (1982) used the older name Clausocalanoidea Giesbrecht, 1892, for the Pseudocalanoidea Sars, 1902. The morphological characters used by Andronov (1974) in dividing the Calanoida into the 9 superfamilies are (1) the separation or fusion of the 8th and 9th segments of the antennule, (2) the geniculation of one of the antennules in the male, (3) the number of setae on the 2nd and 3rd endopodal and the 3rd exopodal segments in the 3rd and 4th swimming legs, (4) the development of the mouthpart appendages in the adult male, (5) the presence or absence of an outer seta on the basis of the 1st swimming leg, and (6) the presence or absence of aesthetascs on the geniculated antennule of the male. On the basis of these characters, Andronov proposed phylogenetic relations of the 9 superfamilies.

In the present study, these and some additional anatomical features are extensively examined to determine the phylogenetic relations among various superfamilies. Characters believed to be useful for the construction of the phylogenetic relations are briefly described below. The body of the Calanoida is very uniform in shape throughout the group but variable to some extent in the number of free segments in the metasome and urosome. The head and the 1st thoracic segment bearing maxillipeds are always fused forming a cephalosome or cephalon. The 2nd to 6th thoracic segments, each bearing a pair of swimming legs and thus often termed pedigerous or simply metasomal segments, are all separate in the primitve groups but the first 2 or/and the last 2 segments are usually fused in the advanced groups, such as the Clausocalanoidea. The urosome in the primitive forms is typically 5-segmented in the male and 4-segmented in the female. The fusion between urosomal segments is more commonly found in the females of the advanced groups than in the males.

The antennules are found to be very useful in classifying the Calanoida, those with 25 free segments are considered the most primitive condition, and the fusions between various segments occur in the specialized groups. The most important characters of the antennule are the separation or fusion of the 8th and 9th segments in both the female and the male and the geniculation often found in one of the male antennules. Whether one of the male antennules is geniculated or not and, if so, which side of the body bears the geniculated one is known to be very consistent in a given group of copepods. In the family Metridinidae, however, it has been found that the geniculation may occur either on the right or on the left side depending on the individual copepod (Ferrari, 1984).

In the antenna, it is the segmentation of the exopod that shows consistent differences among various groups of the Calanoida. Primitively, the exopod is 10-segmented, each segment bearing a seta except for the last which carries 3 terminal setae. The Augaptiloidea is characteristic in having 9 segments, instead of 10, on the antennal exopod. Judging from the setation of the appendages, none of these 9 segments seemed to have been formed by fusion of 2 or more segments. The antennal exopods of the Pseudocyclopoidea also seem to be basically 9-segmented, but the picture is obscure due to the fusion between various segments. In all other superfamilies, however, the exopod is basically 10-segmented, of which the 2nd to 4th and 9th and 10th segments are always fused except for the Eucalanoidea, in which the last 2 segments remain separate.

The mandibles are basically the same in all the superfamilies, with a strong masticatory blade developed from the coxa and a 5-segmented exopod and a 2-segmented endopod attached to the basis. The maxillule consists of the coxa bearing 3 inner and 2 outer lobes and the basis followed by 2 rami, the endopod and the exopod. The 2nd outer lobe, represented by a single seta, is present only in the Centropagoidea, the Megacalanoidea, and the Eucalanoidea. There are two obvious trends in the evolutionary changes of the maxillules. One of these is found exclusively in the Augaptiloidea, where the exopod shows a progressive outgrowth and gradually comes to occupy the terminal end of the appendage. The other is found in all other superfamilies, in which the exopod shows a progressive reduction in size anbd a gradual shifting to a proximal position on the basis.

The maxilla is generally regarded as consisting of the basipod followed by the endopod. The basipod typically bears 6 lobes each carrying several strong setae. The proximal 4 lobes seem to belong to the coxa and the distal 2 to the basis. The coxa also has a seta on the outer margin, which could be regarded as an outer lobe and is found only in the Centropagoidea, the Megacalanoidea, the Eucalanoidea, the Ryocalanoidea and the Spinocalanoidea. The endopod is rather small, with varying numbers of free segments and typically with a total of 7 setae. The maxilla shows a progressive elongation in the Augaptiloidea, while it generally shows a progressive shortening in the remaining groups. The maxilliped is basically similar to the maxilla, although the endopod is well-developed and distinctly 5-segmented. As in the maxilla, the coxa typically bears 4 lobes and the basis 2 lobes. In the family Metridinidae the coxa also has a seta on the outer margin, which seems to be serially homologous to a similar seta found on the maxilla in certain groups.

The 5 pairs of swimming legs are all basically the same, each consisting of the 2-segmented basipod followed by the 3-segmented endopod and exopod. The evolutionary changes of the legs are generally believed to be traceable by following the trends of reductions in the number of component segments, setae, spines of the appendages. Typically, the coxa has an inner seta, while the basis has an inner and an outer seta. The 3 exopodal segments are rarely fused in the first 4 pairs of legs, and each of the first 2 segments has an inner seta and an outer spine. It is the number of free endopodal segments and that of setae and spines of the last segment in both the endopod and the exopod that shows considerable variations and is believed to be important for the determination of the phylogenetic relations among various groups. Of all the swimming legs the 5th pair is most variable, ranging from the one basically the same as the 4th to the complete reduction of the appendage in the female or to either a highly complicated grasping organ or a simple uniramous appendage in the male. The anatomical complexities of the geniculated antennules and the 5th legs in the male are supposed to reflect their elaborate copulatory behavior.

All the 40 calanoid families classified into 9 superfamilies (Bowman and Abele, 1982) are studied morphologically to reevaluate their classification and phylogeny. The results generally conform to the classification presented by Bowman and Abele. However, the families Epacteriscidae Fosshagen and Spinocalanidae Vervoort, included in the superfamilies Augaptiloidea and Clausocalanoidea, respectively, are recognnized here as separate superfamilies bringing the number of calanoid superfamilies to 11. As discussed below, the Epacteriscidae is found to be even closer in details of the appendages to the Pseudocyclopoidea than to the other families of the Augaptiloidea and the Spinocalanidae is closer to the Ryocalanoidea than to the families of Clausocalanoidea. Of the 11 superfamilies recognized here, the Platycopioidea, the Pseudocyclopoidea, and the Epacterisciodea are so highly specialized, probably as a result of their adaptation to the epibenthic habitats, that it is not possible to determine their phylogenetic positions acceptable in the light of prevailing phylogenetic concepts. The phylogenetic scheme proposed here is, therefore, mainly centered on the 8 remaining superfamilies, which are primarily planktonic, and the possible phylogenetic relations between these planktonic and the three benthic groups are discussed later (Figure 1).

Of the 8 superfamilies that are primarily planktonic, the Augaptiloidea is distinctly different from the others and believed to have diverged very early in the evolution of the group. Nearly all of the species belonging to this superfamily are deep-sea forms. The character by which the Augaptiloidea is distinguished from the others are as follwos: (1) the left antennule of the male is geniculated (In the male of the family Metridinidae, however, the geniculated antennule is known to occur either on the left or on the right side.), (2) exopodal segments 1-7 of the antenna are all separate, (3) the exopod of the maxillule is elongated, (4) the maxilla is long with a well-developed 6th lobe on the basipod. The Augaptiloidea has many primitive features, such as the separation of all 25 segments of the antennule, the 3-segmented endopods and exopods in all 5 pairs of swimming legs, the male 5th pair of legs that is only slightly asymmetrical and the presence of a well-developed outer seta on the base of some of the swimming legs.

After the separation of the Augaptiloidea, all the remaining superfamilies can be grouped into a monophyletic assemblage by means of several common characters found, of which the fusion of exopodal segments 2-4 of the antenna and the geniculation of the right antennule in the male are important. The next superfamily that has diverged from the main line of the Calanoida is the Centropagoidea, which is highly characteristic in having in the male a strongly geniculated antennule on the right side and an extremely asymmetrical 5th pair of legs with the right leg greatly modified for grasping. With the exception of the family Candaciidae, the members of the Centropagoidea are restricted in their distribution mainly to the neritic and freshwater habitats.

The main line separated from the Centropagoidea is characterized by a drastic reduction in the geniculation of the male right antennule and the 5th pair of legs. Its subsequent division gives rise to the Megacalanoidea which is distinct from those groups following the main line in maintaining a number of primitive characters in common with the Centropagoidea and the Augaptiloidea, for example, the separation of the antennular segments 8 and 9 and the 3-segmented endopod and exopod in all 5 pairs of legs. The remaining 5 superfamilies are characteristic in that antennular segments 8 and 9 are fused, the endopods of the 1st have less than 3 segments, and the 5th legs of the female are either uniramous or misssing. (The information on this last character is not available in the Ryocalanoidea.) The group that has diverged first in these 5 superfamilies is the Bathypontioidea which, comprised exclusively of deep-sea forms, is distinct in that the mouthparts are highly modified and in the male 5th pair of legs, the right leg is larger than the left, while the remaining groups still maintain mouthparts that are essentially of the megacalanoid type and in their males the left 5th legs are larger than the right, as in the Megacalanoidea.

The next group to be diverged is the Eucalanoidea, which is readily distinguished by the following characters: the endopods of the 1st and 2nd legs are 2- and 3-segmented, respectively; exopodal segments 9 and 10 of the antenna are separate, and the caudal rami are fused with their anal segment.

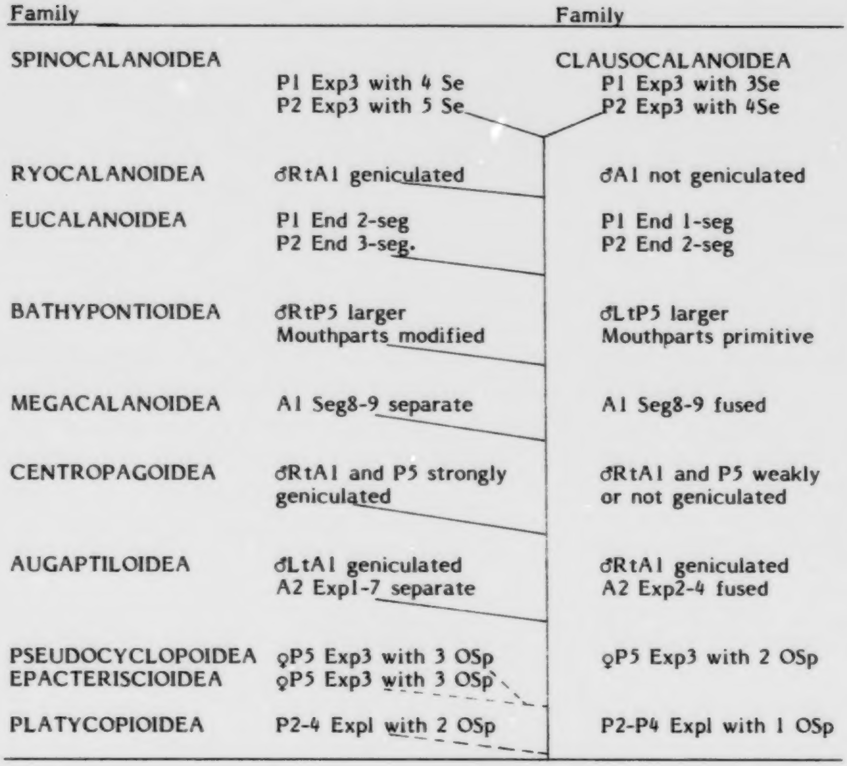
Family
Family
SPINOCALANOIDEA
CLAUSOCALANOIDEA
P1 Exp3 with 4 Se
P2 Exp3 with 5 Se
P1 Exp3 with 3Se
P2 Exp3 with 4Se
RYOCALANOIDEA
♂RtA1 geniculated
♂A1 not geniculated
EUCALANOIDEA
P1 End 2-seg
P2 End 3-seg.
P1 End 1-seg
P2 End 2-seg
BATHYPONTIOIDEA
♂RtP5 larger
Mouthparts modified
♂LtP5 larger
Mouthparts primitive
MEGACALANOIDEA
A1 Seg8-9 separate
A1 Seg8-9 fused
CENTROPAGOIDEA
♂RtA1 and P5 strongly geniculated
♂RtA1 and P5 weakly or not geniculated
AUGAPTILOIDEA
♂LtA1 geniculated
A2 Exp1-7 separate
♂RtA1 geniculated
A2 Exp2-4 fused
PSEUDOCYCLOPOIDEA
♀P5 Exp3 with 3 OSp
EPACTERISCIOIDEA
♀P5 Exp3 with 3 OSp
♀P5 Exp3 with 2 OSp
PLATYCOPIOIDEA
P2-4 Expl with 2 OSp
P2-P4 Expl with 1 OSp

Figure 1. *The phylogenetic relationships of the calanoid superfamilies.*
Abbreviations: A1, antennule; A2, antenna; End, endopod; Exp, exopodal segment; Osp, outer spine; P1-5, 1st - 5th legs; Se, seta; Seg, segment; Rt, right; Lt, left.

In the remaining calanoids, however, the endopods of the 1st and 2nd legs are 1- and 2-segmented, respectively. The subsequent divergence gives rise to the Ryocalanoidea. So far only the male of a single species has been found in this superfamily (Tanaka, 1956), which is very similar in details of the mouthparts and the 1st to 4th swimming legs to the Spinocalanoidea described below. The right antennule of the ryocalanoid male is, however, clearly geniculated.

The remaining calanoids are finally divided into two groups, the Spinocalanoidea and the Clausocalanoidea. The former is less specialized than the latter in such features as the presence of the outer seta on the maxilla, the 3rd exopodal segments of the 1st leg with 4 setae and that of the 2nd and 3rd legs with 5 setae, and only slightly asymmetical basipods of the male 5th pair of legs. Furthermore, members of the Spinocalanoidea are mostly bathypelagic. In the Clausocalanoidea, however, the maxilla has no outer setae, the 3rd exopodal segment of the 1st leg has 3 setae, that of the 2nd and 3rd legs has 4 setae, and the basipods of the male 5th legs are strongly asymmetrical.

The phylogenetic relations presented above are basically similar to those of Andronov(1974) but the Megacalanoidea is regarded here as an offshoot from the main line rather than as an ancestral group to a subsequent evolutionary divergence as proposed by Andronov, and the Spinocalanoidea is considered a superfamily separated from the Clausocalanoidea, presumably by invading deep-sea habitats. As mentioned earlier, the groups that do not easily fit into the proposed phylogenetic scheme are the Platycopioidea, the Pseudocyclopoidea, and the Epacteriscioidea. These 3 groups show a number of highly specialized features, presumably resulting from their adaptatoion to the epibenthic habitats. The is, however, an important character that is shared by all three groups, that is, the presence of 3 outer spines on the 3rd exopodal segment of the female 5th leg, a supposedly primitive character not found in any other groups of the Calanoida.

The members of the Platycopioidea are unique in having 2 outer spines on the 1st exopodal segment in the 2nd to 5th legs and supposed to constitute a group diverged very early from the rest of the Calanoida. The Pseudocyclopoidea shows affinities to the centropagoid-megacalanoid line in the general anatomy of the appendages excepting the 5th pair of legs in both the female and the male and possibly the antennae as well. The Epacteriscioidea has extremely specialized mandibles, maxillules, and maxillae but shows a close similarity to the Pseudocyclopoidea in all 5 pairs of the swimming legs, although the 5th pair of the legs of the epacteriscid male is more primitive in that the endopod is 3-segmented and both legs are nearly symmetrical with almost no geniculation. In the male of the Epacteriscioidea , however, the left antennule is geniculated, while in the Pseudocyclopoidea it is the right that is geniculated. The antennae also show a considerable disagreement between the two groups. Although Bowman and Abele (1982) included the Epacteriscidae in the Augaptiloidea as a family, they show little resemblance except that the left antennule is geniculated in the male. Therefore, the Epacteriscioidea is here considered a separate superfamily and its closest relative seems to be the Pseudocyclopoidea.

It is interesting to note that most of the superfamilies are separated to a certain extent into different habitats. The Platycopioidea, the Epacteriscioidea, and the Pseudocyclopoidea, which are regarded as most primitive groups, live in close association with the bottom of the sea. The Augaptiloidea, the Bathypontioidea, and the Spinocalanoidea are represented mostly by deep-sea species. The Centropagoidea is a group restricted in the geographical distribution mainly to the neritic and freshwater environments. The remaining superfamilies - the Megacalanoidea, the Eucalanoidea, the Ryocalanoidea, and the Clausocalanoidea - are oceanic, primarily inhabiting the epi- and mesopelagic depths.

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DISCUSSION

Edited by *Z. Kabata*

F.D. Por: I have a few comments. My first comment is related to the antiquity of copepods. In my view, we should definitely think of a very early origin of the copepods and not of a Mesozoic one, as suggested by Brian (Dr. Marcotte). I would refer to a very recent paper on the fossil microcrustaceans from the Cambrian, so-called "ersten Crustaceen", described by Müller. These are obviously microcrustaceans, meiobenthic beasts, very small, millimetre-sized and clearly showing many archicopepodid characters, or characters intermediate between copepods and Ascothoracida. We are clearly dealing with a very, very old, at least Cambrian, group when we speak of copepods.

Now, this brings us to Cambrian environments. It is clear that during the Cambrian the fresh waters were not yet inhabited. So freshwater copepods must be younger. I daresay that the phyto-environment, the algal flora, was not yet developed at that time. In general, modern algae are later than the Cambrian, and of course the pelagic environment, open ocean environment, was not in being in the Cambrian. The algae as we know them are probably Mesozoic, dating back to the time when diatoms and coccoliths appear. Therefore, we have to speak of bottom-living, small animals eating detritus, or whatever was available. I think we cannot go to the present big groups to find something near to the copepods, neither to the cyclopoids, nor the calanoids, and probably not to the majority of the harpacticoids. Since copepods are very old, I think we have to find a few small groups of "living fossils". They might be the mormonilloids or some of the primitive harpacticoids.

It's clear that the calanoids, at least the open sea calanoids, are a new, Cretaceous group. The majority of freshwater cyclopoids, because they show a very nice separation between gondwanic and laurasian groups, are also late, post-Triassic. We might, however, here and there, have also very old inhabitants of fresh-water, of course, probably not earlier than Devonian. They might be parastenocarids or similar groups, and again here we have to find some living fossils. In general, when we speak of cyclopoids, the majority of calanoids and the vast majority of harpacticoids, that is harpacticoids which have grasping P1, grasping maxillipeds, these are late-comers that had arrived after phyto-environments of the globe became well developed. This means they had to be post-Cambrian.

Z. Kabata: Thank you, Prof. Por. Well, we have been shown only yesterday an early Cretaceous parasitic copepod which was extremely well developed. It does take some time to develop this kind of form. This would rather favour the theory of an earlier origin. Perhaps Brian (Dr. Marcotte) would like to say something about that.

B.M. Marcotte: The only comment is that phytoflagellates occurred in the Devonian for the first time, so that there were at least some materials in the phytoplankton for planktonic organisms to ingest. Interestingly enough, the diatoms occurred in the Cretaceous at periods of turbidity maxima, organisms with specialized pigment systems to absorb wavelengths of light that occurred in turbid water, so it kind of buffers the thing. As to the origin of the copepods in the Cambrian, I do not know. I am cautious, though, because copepod-like limbs do occur, for example, in Scourfield's branchiopod-like creature and elsewhere. It could be that at least the thoracic limbs, the swimming-type limbs of copepods, do occur convergently in several crustacean groups. I just don't know enough about the microfossils in the Cambrian, except I haven't seen a copepod there yet. I have seen things that share some say I have seen one. I would more likely expect one in the Silurian-Devonian. In the Silurian you start having a lot of creatures leaving the sea and going into fresh-water. The first freshwater ostracods occur in the Devonian to lower Carboniferous. Things are getting out, I presume, of a turbid ocean, of an ocean that is anoxic and getting crowded, and presumably coastal environments are very competitive at that point, if they were not before. I don't know.

J.-S. Ho: I have some comments to make on that. The palaeontologists tell us of the so-called Permo-Triassic bottleneck. This means that between 80% and 95% of marine organisms died off during that period, let's call it Permo-Triassic. In other words, only very few marine organisms made it through the Palaeozoic and into the Mesozoic. Whether the copepods are one of the surviving groups we do not know because we don't have the fossil records. Therefore, if we must rely on the fossil records, I would say it is hopeless.

B.M. Marcotte: I think you can. There is this notion that the Permo-Triassic boundary extinguished all kinds of organisms. In fact it didn't. The extinction of most filter-feeding organisms, most organisms dependent upon symbiotic algae (or at least presumed to have been dependent upon them), the complementary origin of deposit-feeding bivalves, the extinction of visually foraging organism, whether they are nautiloids or trilobites, all begin at the Ordovician and continue without interruption to the Permo-Triassic boundaries. It is true that there was something that stopped a lot of organisms, like trilobites, but things that were foraging visually, or filter-feeding, were having real problems long before, 150 million years before and longer. This gets back to this notion that oceans may have been getting more turbid, that vision was becoming a limiting resource for foraging, filter-feeding was a problem and animals became deposit-feeders or chemoreceptive. The last of the trilobites to exist with primitive eyes were in clear tropical waters. So, at any rate, there is more to the story than simply an extinction at the Permo-Triassic boundary. There is a great lot of detail, if you look at sensory modalities instead of looking only at the number of genera. You see a lot more of what has been going on earlier.

Z. Kabata: Geoff (Dr. Boxshall), have you any comments?

G.A. Boxshall: I would have to agree on the ancient origin of at least an ancestral type of copepods. Müller found some very interesting microcrustaceans in his Cambrian-Austin. The nauplius stage of one of them will be shown tomorrow in Geoffrey Fryer's talk. I oppose Maxillopoda as a taxon. There are taxa described by Müller in 1983 that conform precisely to the 5-6-5 cephalon-thorax-abdomen (or 5-7-4, depending on how you divide the trunk into thorax and abdomen). Both of these can be accommodated into the maxillopodan plan. There are animals in Müller's paper which have exactly this plan: a cephalon of 5 segments, with 5 paired appendages and a large labrum; there is a thorax with 6 pairs of biramous thoracopods, and there are 4 or 3 segments in the urosome, the first of them bearing the genital openings. No, I don't like the Maxillopoda, but you can't argue against the facts.

Z. Kabata: Thank you. Does it exhaust our discussion of this question? Dr. Schminke?

H.K. Schminke: The trouble is, we all think they are Crustacea, these ones that have been discovered by Müller. In fact, Lauterbach is beginning to question whether they are really Crustacea. Now, what are the synapomorphies of Crustacea? Really, what are the definite characters that define Crustacea as opposed to the rest of the arthropods? When you go back and include the fossil forms, it becomes very difficult to define Crustacea. I mean, there are lots of characters by which we define Crustacea but most of them are plesiomorphic if you compare them. I can't go into the details of Lauterbach's analysis, still it is not always quite clear whether all these forms we now call Crustacea are really crustacean. Before we use them in our discussions, we have to wait and analyse them and see if they are not something else. Because actually they are very far back in times when Crustacea evolved. Perhaps they were other groups which were near to the crustaceans or sister groups to Crustacea. Consequently, I think they don't tell us very much for the moment. Brian (Dr. Marcotte) said, that in the Permo-Triassic we had only large crustaceans. When I visited Müller in Bonn, he told me that he discovered them also in other periods of the Earth's history, I mean not only back in the Devonian. These minute things have been discovered also in later deposits. So, small crustaceans have always been there. It is not as if we had small ones, then bigger ones and then, by neoteny, smaller ones again. Being small is certainly an advantage, I agree with you. But neoteny is not the only way to become small. So I don't think this is convincing evidence that neoteny plays an important role in becoming a copepod. We should always keep in mind that there are quite different means for becoming small. Another thing is that, for example, Tisbe could be a model for a very primitive crustacean. You said that when they feed, their mouthparts look pretty much the same as the mouthparts of other groups, but this could be convergent. I think that similarity just doesn't tell us they are the same or that this is something that could be ancestral to other types. I think we have to look deeper into this and find new evidence, such evidence, for instance, as that Geoff (Dr. Boxshall) had proposed today. It is so difficult and there are so many aspects relating to different talks today that I do not know how we should proceed. Perhaps we should discuss different talks, one by one. How should we proceed?

Z. Kabata: If we do that, we will inevitably leave something out of the discussion. Perhaps we better let anybody with anything particularly pressing on his mind speak out, whatever the topic. Unfortunately, whatever we do, we are not going to cover everything. Dr. Björnberg, you had a question?

T. K. S. Björnberg: It is unfortunate that during all this discussion no one mentioned nauplii. It is unfortunate, because nauplii bring in evidence which in a way goes completely against a lot of what Andronov proposed. For instance, Clausocalanus, Microcalanus, Ctenocalanus, Calanus and all the calanids and paracalanids, all have the same nauplius. I am sorry, I have not discovered this. This was discovered by Oberg in 1906, and there is the work of Marshall and Orr, Mary Lebour and of many old-timers who worked on all these nauplii. They have been known at least since 1906. They are exactly alike, even their musculature is alike. They move in the same way. I cannot believe that there was a convergence of naupliar forms in these different species and genera. They can only be distinguished at first sight by their size and even then one has to look well at them, because there are several genera that have nauplii of the same size. This is why I think that there is something wrong with Andronov's classification. I am sorry to be repetitive, but you do have to look at the nauplii. When you do, you find that you cannot separate Clausocalanus and clausocalanids from the calanids and paracalanids. Calocalanids also have the same nauplius, but it is a little longer than the rest, so that it moves a little differently. It is not top-heavy like the nauplii of Calanus, Clausocalanus, Danocalanus and Paracalanus. It does not somersault but rather moves a little way and then gives a little somersault; then it does it again in the same way. So, if you want to separate anything, you might separate calocalanids. I would not do it myself, I think they are well placed together with paracalanids and calanids. The one group that from the point of view of nauplii cannot be broken up are the clausocalanids. They must belong together in one group with Calanus and Paracalanus and (if you do not want to split) also Calocalanus. Unfortunately, Megacalanus has no known nauplius. At any rate, once you know that these nauplii are so very much alike, it would be going a bit against the evidence of nature to separate animals with identical developmental stages. According to Williamson, and he has been generally acknowledged for his work on larvae, it is absolutely important that one considers all stages of development when one studies taxonomy of anything at all. I try to defend my nauplii by saying that most of the copepods in the world never reach the adult stage, they are eaten while still in the nauplius stage. A good reason why nauplii should be considered. There is one more thing: If you want to split anything, there is a big group that is considered homogeneous but on naupliar evidence is splitable. You can split the eucalanids. This group has two different nauplii, completely different even in their movements, their behaviour and their musculature. On the one hand, you have Rhincalanus and Eucalanus, the Eucalanus elongatus group which has nauplii derivable from those of the calanids. Hence, they must be very closely related to the calanids. On the other hand, you have Eucalanus pileatus, Eucalanus crassus which Fleminger placed in a different group. He set up four groups: Eucalanus elongatus, E. attenuatus, E. pileatus and E. subtenuis. The E. elongatus group is completely different from all the others because it has a nauplius exactly like that of Rhincalanus. There are minor differences between them only in the symmetry of the mouth. All the others have nauplii definitely far more similar to those of Centropages. The adult forms must have converged, because the nauplii are completely different, even in their movements.

Z. Kabata: Hands are rising all over the place. I think I should ask Dr. Park to comment, because calanoids were his subject. Perhaps he has a short comment.

T. S. Park: I do not have much experience with the nauplii. I really cannot make any valid comment because Dr. Björnberg has already substantiated her own evidence. However, I believe that the planktonic stages have their own specializations or their adaptations. As far as I can see, nauplii are simple when compared with adults. I believe that the adult structures also show a great deal of specialization, but if we select certain appendages we will find that primitive features are maintained by all groups. Only certain groups show some similarity of synapomorphies. Those similarities are similar specializations and they can be selected for classifying or for tracing phylogenies.

Z. Kabata: Thank you. Geoff (Dr. Boxshall), have you a comment?

G. A. Boxshall: I think you (Dr. Björnberg) are tending to fall into a trap in reverse to that we are falling into. You base your conclusions on nauplii, we do ours on adults. We obviously have to meet halfway. But I am very suspicious in many ways of naupliar evidence, because not so many are well known. In your lecture the other day you drew attention to the fact that nauplii of Longipedia and Canuella were sufficiently different to separate them from all the other harpacticoids, perhaps even to remove them from the group. Or am I taking it further than you would? When you consider the adults, there are good synapomorphies that link the harpacticoids together. Primarily the fusion of the endopod and the basis in the fifth leg, which forms a baso-endopod. It is a structure unique to the harpacticoids, is present in the longipedids and canuellids and in Oligoarthra, the other harpacticoids. It is a good, clean synapomorphy. On the other hand, some of the factors that we are looking at and that make longipedid nauplii so different are all plesiomorphic. If you adhere to a cladistic methodology, you cannot construct phylogenies on primitive characters, you have to look for advanced ones. There are enough advanced characters to produce a scheme of relationships for all the eight copepod orders. I think we ought to look at the nauplii as well and see if they have synapomorphies that support these arguments. But, looking at the adults we know there are synapomorphies to link them all in coherent, congruent (I use an "in" term) scheme.

Z. Kabata: Dr. Schminke, you have a comment?

H. K. Schminke: Actually, I want ask a few questions. Now, Dr. Ho, could we take another look at your "straw man"? (My first question about synapomorphies of harpacticoids has already been answered.) Now, it shows that you have synapomorphies mostly on the right-hand side. Let us take the Cyclopinidae the first family what is the synapomorphy of that family, because without one it is not a clear monophyletic grouping.

J.-s. Ho: I was asked to do this back in March. I did not have much time to go through all characteristics I could pick. So I restricted myself to the cephalosomatic appendages, that is why I have in the list from the first antenna all the way down to the maxilliped. I didn't take into consideration the swimming legs, fifth leg or any other characteristic. So if I have those, I think it will show somewhere here. On this line, on that line of the archinotodelphyids, on the line of the notodelphyids. By the way, in the notodelphyids there you can plug one in, right there, which is the brood pouch. That is the only one which has a brood pouch. None of the others have it. This is just an indication that if I have enough or many characteristics I can show something there. The time limit did not allow me to go through them all.

K. Schminke: All right, this is, then, a preliminary scheme, isn't it? It is a preliminary system, because if you have on the other side antenna two without exopod, this reduction is not a very strong character in my opinion. Yet, you have a lot of conclusions drawn from this table. This is why I thought it was more important than it appears to be now.

J.-S. Ho: In answer to your question about the reduction of the exopod in the second antenna, it came up because I made a comparison with the misophrioids and they have the exopod, which this group doesn't have. This showed the synapomorphy of the entire cyclopoids.

H.K. Schminke: Geoff, I have a question for you. You said that the Siphonostomata are monophyletic. Yet there are other people who say they are polyphyletic. Now, how many species of siphonostomes have you studied? I believe the way to do it would be to ask the people: which are the different groups that are considered to have originated polyphylogenetically, and then study one species in each of these groups. If they show the character you have shown, I think I will be convinced. But just one, (it is only one that you have studied, isn't it?) cannot be accepted as a definitive end of the discusssion.

G. A. Boxshall: That is a rotten question. I have looked at three. One of them is somewhat primitive, Hyalopontius is definitely more primitive than Pontoeciella which is an invertebrate-inhabiting form, and caligids. Those two from the two different categories of host type can be linked together as advanced siphonostomes, and the other one is a plesiomorphic siphonostome. There are other characters that link the siphonostomes, they do have another synapomorphy in the entire phylogenetic scheme. If you have taken off some of your other groups first, by the time you get there, there is another one and that is your exopod again, of the antenna.

F. D. Ferrari: I would like to ask the panellist to look into the future instead of the past and think along other lines. Several years ago Max Hecht wrote an important paper on the evolution in which he suggested that the patterns of reduction contained the least evolutionarily significant information, especially if the underlying genetic systems are widespread, leading to many parallel origins. We also today have widespread evidence of the genetic systems which can add elements in arthropods. So, looking into the future 100 years from now, when your sons and daughters sit here to analyze copepods, will they still be making use of somewhat evolutionarily uninformative seuqences of reduction?

G. A. Boxshall: In our little postscript from Amsterdam we said that the implicit assumption is made that evolution in copepods and Crustacea generally proceeds through reduction, fusion and loss. I agree. Hecht said in that NATO paper that reduction and loss are the worst categories of character that you can use, but there is nothing else. Evolution seems to go that way. There is very little evidence of the addition of novel structures in the evolution of copepods, such structures as there are tend to be rather small and specialized like the pigment blob in Pleuromamma and various other particular items you can choose but say the fifth leg of the calanoid male. It is a highly modified, specialized grappling apparatus but it hasn't any additional elements. It's got superficial complexity superimposed upon its existing trimerous, biramous structure. It has no new elements as far as I am aware.

F. D. Ferrari: That escapes the point. The point is we can have reduction and then a re-addition and I think that there are genetic factors that enable you to do that.

G. A. Boxshall: If you say evolutionary reversals are commonplace then I say that until we have evidence from the geneticists and biochemists that this is common we have to take things at face value. Otherwise you have no system at all.

I have a phylogenetic scheme for the whole Copepoda based almost solely on reduction characters.

Voice from the floor: Could you tell us about it?

G. A. Boxshall: That was not a planted question, Mr. Chairman, is it appropriate to show this scheme as another "straw man"(Fig. 1)?

Z. Kabata: Please do.

G. A. Boxshall: One or two people have already seen this, but I have made some slight modifications. It has been pointed out to me that I have my basi-endopod in a wrong place, but we will get to that. Right.

Character 1. The apomorphy for the Calanoida is the prosome-urosome articulation position. It's a good character for the Gymnoplea and it serves to diagnose the Calanoida. Character 2, therefore, is going to be the differing position of the prosome-urosome articulation in Podoplea; the latter comprising the rest of the Copepoda. So far no reduction. Character 3, there is a reduction. This is a loss of a separate distinct coxoexite on the first maxilla. Calanoids have one, it doesn't have an articulation but it has a suture at the base and it has a muscle, an extrinsic muscle that originates up in the body and passes right through the precoxa-coxa and into the exites. In all podopleans the exite is incorporated into the coxal segment. In many of the groups you have a cluster of setae there but in none that I am aware of do you have a suture line separating the exite from the coxa. The misophrioids (I did not put them all in) have the carapace and that will do. I thought that the separation of misophrioids as a sister group of the rest of the Podoplea was going to be a problem, but I found three characters which I was very pleased with at the time, though I discover now that it should only be two. First is loss of the heart. The heart is retained in misophrioids and calanoids but none of the others have a heart - Character 4. Character 5 is the loss of a separate articulated endopod on the fifth leg. One misophrioid, Misophriopsis, has this separate endopod, none of the others do. Character 6 is the fusion

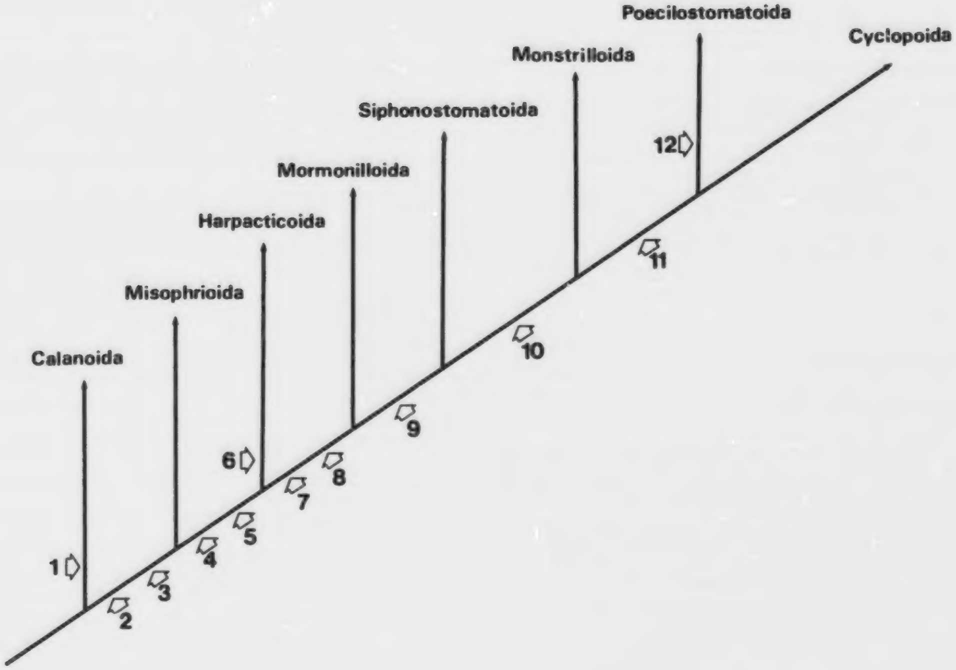
Poecilostomatoida
Cyclopoida
Monstrilloida
Siphonostomatoida
Mormonilloida
Harpacticoida
Misophrioida
Calanoida
12
11
10
9
8
7
6
5
4
3
2
1

Figure 1. *Significant characters in copepod phylogeny*

1. *Prosome-urosome junction between thoracic somites 6 and 7*
2. *Prosome-urosome junctions between thoracic somites 5 and 6*
3. *Loss of separate maxillulary exite with basal suture*
4. *Partial fusion of gential somite and first abdominal somite to form genital double somite with suture*
5. *Loss of heart*
6. *Possession of baseoendopod on fifth leg*
7. *Complete fusion of genital and first abdominal somites to form genital complex without suture*
8. *Loss of endopod of fifth leg*
9. *Reduction of antennary exopod to 1 segment*
10. *Loss of antennary exopod*
11. *Female genital openings lateral or dorsolateral*
12. *Falcate mandible*

of what's left of the endopod with the basis so the baso-endopod is in fact a synapomorphy of the harpacticoids. Here, where I have it, it becomes a synapomorphy of all the rest; it is lost later on. Characters 7 and 8 are synapomorphies for all the rest. Seven is the complete fusion of the genital segment and the first abdominal segment. To my knowledge in all of these, from the harpacticoids onwards, there is no suture line separating these two segments. They completely fuse into a genital complex. They are partially fused in the harpacticoids, but you often have a suture line left, indicating quite clearly that it was a functional articulation fairly recently in their ancestry. Character 8 is a non-starter because I had to move the baso-endopod, but we have one synapomorphy there that is a reasonable one; it is a fusion not a loss. We have removed the first three and what we are left with is a mixture of three well-defined groups: the mormonilloids, these funny, little, planktonic, sexless jobs; the monstrilloids which we haven't mentioned, a token parasitic group. Their nauplii are internal parasites of polychaetes and the adults are free-swimming and planktonic. You can't use them much because they have a first antenna and swimming legs and nothing in between. However, character 9, which is a synapomorphy linking all these and separating the mormonilloids, is the reduction of the antennary exopod to at most two segments. In fact, I think it is an exopod reduced to one segment. I don't know of examples of two but there are possibilities. Mormonilloids still retain eight. They still have a very well developed antennary exopod. Now it starts to get a bit tricky. In siphonostomes we have a synapomorphy for the mandible, but I found it rather difficult to separate from here clearly. Character 10 which I have to use with apologies is the loss of the antennary exopod. Poecilostomes, cyclopoids, and monstrilloids do not have an antennary exopod. The logical flaw here is that monstrilloids do not have an antenna, but when you are desperate you will use anything. The monstrilloids have not really been incorporated into any coherent system, because they lack so many characters. What characters they do have tend to be unique. Character 11, and I was not too sure about it, for me was the lateral or dorsolateral position of the genital openings of the female. Cyclops, if you can visualize it, has these paired egg sacs coming out dorsally. The ancestral plesiomorphic position of the copepods is ventral genital openings. Poecilostomes and cyclopoids, as far as I am aware (and that's not very far) have either lateral or dorsal, or maybe that is a mixed character, but not ventral, anyway. That brings us right up to the poecilostomes and cyclopoids. As Prof. Stock has said the separation here is not particulary clear. I just have this falcate mandible, the lash of the mandibular gnathobase, but the order of separation might only be subordinal if all of these are ordinal, but there are clearly two lineages there. It ist just a question of disagreeing at what level they should be classified.

I am prepared to be shot down now, because there is a number of groups that I know almost nothing about.

Dr. Z. Kabata: Any comments?

T.K.S. Björnberg: I think in all this we haven't yet considered an important factor, which is that the oldest group in the world will not show any more primitive forms. It will present a lot of forms which are extremely adapted to different niches and it also has the greatest number of species. It has had time to adapt to the pressures of the environment and to different kinds of habitats and different modes of life. I think this is something we should think about and not only from the naupliar evidence but also from the number of species. The nauplii of the cyclopoids, the Poecilostomatoida and the Siphonostomatoida are very much alike. They are also most primitive, from the point of view of the Urcrustacean. Judging by the number of species that form this group, which has now been separated into three, if I were asked to vote which one is the oldest: the Calanoida, Harpacticoida or the Cyclopoida plus Poecilostomatoida and Siphonostomatoida, I would vote for the last one because they have the greatest number of species adaptations. They have invaded all the possible habitats and they are well established in all of them. They have invaded the free living marine ambient, they are parasitic and commensal, they are also found in freshwater in great quantity, and they are living in the benthos. This is something to think about.

Z. Kabata: Thank you Dr. Björnberg. You have touched upon a fascinating topic. We are talking now about rates of evolution and various other things. Would anybody like to comment? Prof. Por, you wanted to comment?

F.D. Por: Just a question. You know that I like my Canuellidae very much. They are supposed to occupy a primitive position. What do you think of the separate thoracic segment?

G.A. Boxshall: The segment bearing the first leg? It is entirely separate in the misophrioids as well.

F.D. Por: All right, but this puts the Canuellidae in a position separate from other Harpacticoida.

G. A. Boxshall: None of these characters refer to the incorporation of the first pedigerous somite.

F.D. Por: But you could use it.

G.A. Boxshall: It is too convergent, it happens in all the lineages that I know of.

F.D. Por: I see. Thank you.

Z. Kabata: There are two or three more comments. Dr. Schminke, please.

H.K. Schminke: I would like to comment on Dr. Björnberg's remarks just now. She was saying that because they had radiated into all habitats, they should be the oldest. Now, look at other groups of animals. If for instance you look at the mites, within the Arachnida they are certainly the group that has radiated the most, yet it is not the most primitive. Also you can take the flies within the insects. Flies have radiated practically everywhere yet they are not the most primitive and oldest insects. And take the ophiurids among the echinoderms, which are the most widespread in different habitats and, as far as I know, are not the most primitive. So I don't think that radiation is a good sign for telling us which should be the oldest and which should be the youngest. It's just a matter of striking the right situation and the right time and they radiate into these niches regardless of the period when this has happened.

Z. Kabata: Thank you Dr. Schminke. We have time for two or three more questions, or comments. Dr. Hulsemann, please.

K. Hulsemann: I think that one could argue the other way around and say if a group has spread very much these are all members of the groups that are still surviving and if we have just one or two of a group or very few numbers, others may have died off. So, it would be just the opposite.

D. Soto: It seems to me that all the apomorphies in this case are reductions and fusions, so you can almost predict that the future evolution of the copepods is going to a very simple situation, almost a one cell condition. There is no place for reversion, it seems. I wonder if some of the problems are because of that, because reversions have not been considered as an evolutionary possibility.

G.A. Boxshall: I am open-minded. I can consider anything but you have to work with the characters you have. It is possible there are reversions but what can you do? You have to use the characters there are. If you find other characters that are better, that show noncongruents and therefore convergence or reversions, that's fine. You have to set up to disprove it and the onus is on you to disprove it, otherwise we will have no system at all. I agree some of the characters down here (in the diagram) are reasonable, they are fusions. You can at least work out the homologies when you have got fusions. In the first antenna you have armature elements that can help you to identify what segments you are dealing with, it can give you homologies right through. For example, in the vast majority of calanoids the primitve segments 2, 3, and 4 are all fused into a triple segment, and segment 2 has three sets of armature elements. Now, these are really nice homologies that link some of the groups, but there is nothing else. I have puzzled over this long and hard, 20 minutes. I really couldn't come up with anything else.

J.-s. Ho: This character reversal and the homoplasy which is a synonym of convergence and parallelism and used to be a "systematist's nightmare" are the things we would like to forget about in doing cladistic analysis. Recently they have been trying to take that into consideration, so I think that in perhaps 2 or 3 years from now we will see that there is a good way of analyzing character reversal. How do we explain when it happens?

Taisoo Park: In calanoids, of course, specialization seems to be the trend, but the crucial thing is the reduction of the appendages, the same time there is an increase in the complexities within a group. Such as the undinellids. If you know male Undinellidae, you know that they are primitive in every aspect, but the male's leg is enormously complex as it is also in the Centropagidae. Centropages retains very primitive features, but there are many species in Centropagidae, including the species that I have studied, Epilabidocera, in which the antennules and the fifth pair of legs become extremely complex. These complexities go in parallel with increased complexity of behaviour.

Z. Kabata: Thank you. We have time for only one more question. Dr. Sieg.

J. Sieg: I would like to make a comment on reduction. I think it is very bad when people start to think that structures which have been lost may come back. I have seen many such structures that I had been told have come back, but wherever I have analyzed these structures very carefully, I have found that they were different structures of quite different origin. So they were not homologous. As we normally have to compare characters, we always have to compare homologous characters and not analogous ones. If you pick the wrong structure and compare it with another one you will never arrive at a system which works.

Z. Kabata: Thank you very much, Dr. Sieg. I am afraid that we will have to terminate this interesting discussion.

Contributed Papers

DISTRIBUTIONS OF SIPHONOSTOMATOID COPEPODS PARASITIC UPON LARGE PELAGIC SHARKS IN THE WESTERN NORTH ATLANTIC

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Abstract: Results of field collections in the western North Atlantic indicate that the assemblage of siphonostomatoid copepods which parasitizes large pelagic sharks is made up of species which each exhibit relatively high degrees of host and attachment site specificity. Given the wide ranging lifestyles of large pelagic predators, it is difficult to ascribe possible mechanisms through which host specificity is realized. Attachment site specificity, however, seems an easier matter to contemplate when one closely examines the variety of subtrates presented to the copepod by its shark host. As attachment to the host is a major concern both temporally (considering individuals) and in an evolutionary sense (considering species), the physical interaction between the host substrate and a copepod's attachment structures may be responsible, through the limitation of suitable attachment area, for the site specific distributions of these parasites on sharks.

The literature contains numerous reports of parasitic copepods infesting sharks. Regretfully, however, the scientific value of many must be considered dubious. For one, the remarkable morphological similarities many shark species exhibit along with their morphologically and behaviorally mediated avoidance of museum jars has made the specific identification of certain sharks difficult. No doubt parasitologists have and will misidentify some sharks. Similarly, participation on research cruises has taught me that amidst a pile of thrashing, snapping sharks on a rolling deck, well-meaning fishermen and biologists can neglect to thoroughly and/or accurately record field data when collecting parasites. Furthermore, I contend that when systematics or taxonomy become the main thrust of field collections, all too often parasitic copepods are hurriedly and/or routinely pried from their hosts overlooking interesting bits of information about how these splendid crustaceans cope within their worlds. All in all, problems as aforementioned appear to have generated a shark copepod literature base wherein trends concerning host and attachment site specificity have been masked or left relatively unapproached. This directly contrasts reports of the high degree of host and physical niche specificity exhibited by other ectoparasites of fishes, especially the Monogenea of relatively smaller teleost fishes (Rohde, 1982), and could be interpreted as an indication that shark - copepod interactions are governed by a different set of generalities than those commonly accepted for other taxa of ectoparasites and their hosts.

In this report I will discuss portions of a data set representing collections of parasitic copepods I have taken from large pelagic sharks over the past 7 years in western North Atlantic waters (Fig. 1). In particular, information concerning host and physical niche specificity of representative copepod species will be presented and discussed along with observations on apparent morphological adaptations to apparently preferred or otherwise realized physical niches. Host identifications for these collections were made by National Marine Fisheries Service biologists involved with The Cooperative Shark Tagging Program. Nomenclature for copepods and common names of sharks are in accordance with Kabata (1979) and Robins et al. (1980) respectively.

Thirty species of siphonostomatoid copepods are represented in the data set herein discussed

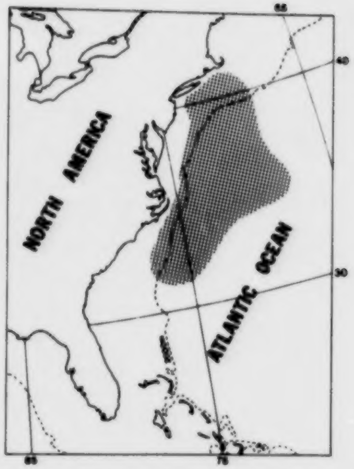
NORTH AMERICA
ATLANTIC OCEAN
65
40
30
85
75

Figure 1. *Location of study area (shaded) relative to North America and 2000m isopleth.*

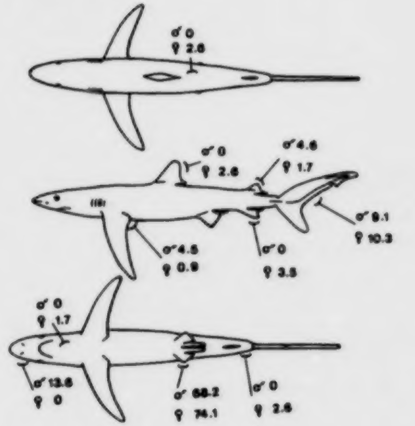
♂ 0
♀ 2.6
♂ 0
♀ 2.6
♂ 4.6
♀ 1.7
♂ 9.1
♀ 10.3
♂ 4.5
♀ 0.9
♂ 0
♀ 3.5
♂ 0
♀ 1.7
♂ 13.6
♀ 0
♂ 68.2
♀ 74.1
♂ 0
♀ 2.6

Figure 3. *Distribution (percent occurence) of male and female Echthrogaleus coleoptratus on 24 blue sharks captures in the western North Atlantic. N(males) = 22, N(females) = 116.*

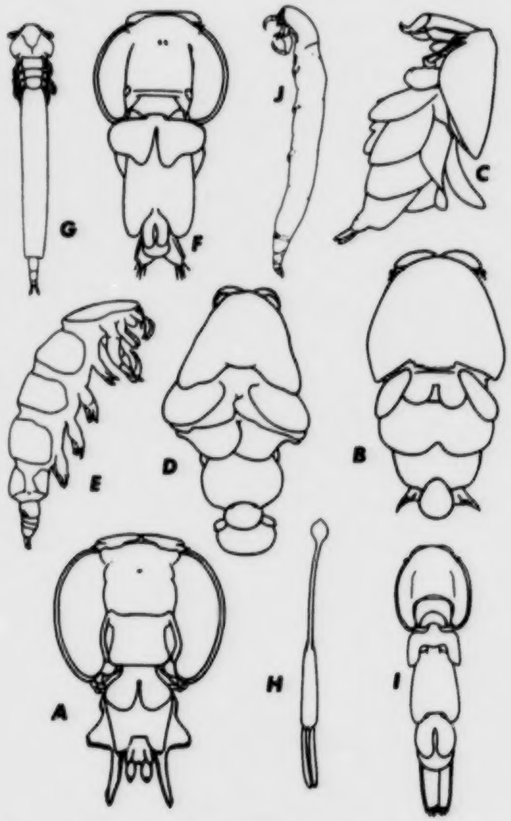
G
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Figure 2. *General habitus of some female siphonostomatoid copepods parasitic upon western North Atlantic sharks. A, Alebion crassus; B, Pandarus smithii; C, Anthosoma crassum; D, Phyllothyreus cornutus; E, Nemesis robusta; F, Dinemoura latifolia; G, Kroyeria carchariaeglauci; H, Optima exilipes; I, Pagina tunica; J, Bariaka alopiae. Figures redrawn from following sources: A, Cressey (1972) and Lewis (1966); B, Cressey (1970); C, D, E, Kabata (1979); F, Hewitt (1967); G, Shiino (1957); H, Wilson (1908); I, Cressey (1966).*

(Appendix I). Some of the physical variation amongst these species is depicted in fig. 2. Host specificity analysis will be restricted to members of the families Euryphoridae (e.g., Fig. 2A), Pandaridae (e.g.,Figs. 2B, D, F, I), and Dichelesthiidae (e.g., Fig. 2C) as their species are difficult to overlook in the field because of their relatively large sizes and habits of typically attaching to hosts' external body surfaces, or in the buccal or branchial chambers. As there is no apparent relationship (direct) amongst shark species between number of hosts examined and number of copepod species collected (Appendix I), the sample size of this study is considered adequate for this analysis.

If we consider the number of host species and genera infested by the 20 represented members of the three aforementioned families we find that 50 percent specifically infest one host species (Table I). These results suggest even higher degrees of host specificity than those recently reported for copepods parasitic upon the world's scombrid fish fauna using similar analysis (Cressey et al., 1983). However, it should be noted that the levels of host specificity presently reported may appear somewhat inflated due to the relatively local nature of the field collections (i.e., not all of the world's shark fauna inhabits the western North Atlantic). Nonetheless, it appears that while locally several species of siphonostomatoids could be considered to exhibit a phylogenetically wide range of hosts (e.g., Pandarus cranchii and P. smithii), many species exhibit high degrees of host specificity. These results are corroborated by Cressey (1970) if his data collected from sharks in the eastern Gulf of Mexico is subjected to similar analysis (Table I). It is interesting to note changes in the relative degree of host specificity of certain species (e.g., Nessipus orientalis, Pandarus floridanus, P. smithii, etc.) between host range analyses for the western North Atlantic and eastern Gulf of Mexico. Such changes may be related to geographic differences in host fauna (species and/or populations) and/or environment (e.g., nearshore versus offshore or temperature versus tropical). If a host range analysis is entertained on a more global level using records from synoptic literature (Table I), again several species exhibit high degrees of host specificity, however, relatively more are depicted as generalists. While the increased sampling effort (both numbers and locations of collections) of a synoptic data base presumably should benefit analyses of overall host specificity, often problems in taxonomy (of both hosts and parasites) seem to relegate many species to generalist status. Recently, Cressey et al. (1983) noted similar problems in dealing with synoptic literature concerning copepods parasitic on scombrid fishes.

Host specificity of various copepod genera calculated as percent specificity (i.e., the percent of species with only one host, as modified from Price, 1980), depicts a range of associations from tight specialists (e.g., Gangliopus and Pagina) to generalists (e.g., Perissopus) (Table 2). Again, these results compare quite favorably to those similarly calculated for various copepod genera infesting scombrid fishes (Cressey et al., 1983).

Host occurrence and percent specificity, however, do not always give true renditions of host specificity. Even though some species of copepods may be found on numerous hosts, very often one or a few host species appear to be infested to a disproportionately high degree (considering either percent occurrence and/or density of parasites). Rohde (1980) developed several indices of host specificity which take such factors into account. These indices theoretically span from 0 (no host specificity) to 1.0 (absolute host specificity), when calculated for species herein considered they almost invariably suggest high degrees of host specificity regardless of host range (Table 3). Similar results have been reported for Monogenea and Digenea of fishes using this analysis (Rohde, 1980 and 1982).

Table 1. *Host range of pandarid, euryphorid, and dichelesthiid copepods as depicted by three geographically diffrent data sets (letter after entry denotes location); western North Atlantic (A), eastern Gulf of Mexico (M), and worldwide (W).**

No. Host Genera Infested	**No. Host Species Infested**				
	1	**2**	**3-4**	**5-8**	**9+**
1	10A 3M 2W	1A 1W	1W		
2		2A 1W	2A 2M		
3-4			3A	1M 1W	1M
5+				1A 6W	1A 2M 4W

* Data for Gulf of Mexico analysis from Cressey (1970), data for worldwide analysis from synoptic records in Cressey (1967), Hewitt (1967), Kabata (1979), Lewis (1966), and Yamaguti (1963).

Because little is known about early life histories of shark infesting copepods it is difficult to surmise how host specificity is actually realized. Given the minute size of the metanauplius, and the far ranging habits and relatively low densities of pelagic apex predators such as sharks, the prospect of successful establishment for any one copepod seems slim. While endoparasites are notorious for exhibiting enormous reproductive potentials to presumably compensate for life histories with difficult establishment phases (Rohde, 1982), parasitic Copepoda like other ectoparasites (e.g., Monogenea) appear to have a relatively low fecundity (as indicated for copepods by examination of the numbers of young contained in their brood sacs). Some Monogenea are known to exhibit rapid generation times, various trophisms to facilitate host location, and parental care in the form of brooding young (Rohde, 1982). It makes good sense for parasitic copepods of large oceanic fishes to share some of these and/or some additional hitherto unknown mechanisms to assist in host procurement. Hopefully, further research will uncover some of these secrets.

Many species of shark infesting copepods can be found as adults attached at particular body sites, and in fact, this attachment site specificity goes well beyond the habitat descriptions most often noted in the literature as gills, body surface, skin, mouth, nares, etc.. In this study for example, ten copepod species (Pandarus cranchii, Phyllothyreus cornutus, Gangliopus pyriformis, Nessipus orientalis, Bariaka alopiae, Eudactylina sp., Kroyeria carchariaeglauci, and 3 Nemesis spp.) were recovered from what has commonly been referred to as the gills, with blue sharks and shortfin makos often simultaneously playing host to several of these (Appendix I).

Table 2. *Percent specificity (percentage of species with one host species) of some genera of copepod parasites of sharks collected in the western North Atlantic.*

Copepod Genus	Number Species	Percent Specificity
Euryphoridae	(3)	(33)
Alebion	3	33
Pandaridae	(16)	(50)
Pandarus	6	33
Dinemoura	3	66
Echthrogaleus	1	0
Gangliopus	1	100
Nessipus	2	100
Pagina	1	100
Perissopus	1	0
Phyllothyreus	1	0
Dichelesthiidae	(1)	(100)
Anthosoma	1	100

Pandarus cranchii is exclusively found attached to the gill arches when found within the branchial chamber. There, many individuals often align themselves in single file, the genital segment of one overlapping the cephalothorax of the next proceeding. *Pandarus* species are considered parasites of the body surface of sharks, and the gill arches, their surfaces studded with placoid scales, are ostensibly part of the general body surface. The adhesion pads and stout, powerful maxillipeds of *Pandarus* species seemingly provide great advantage on such a surface. *Phyllothyreus cornutus*, also a member of the Pandaridae, routinely attaches to the interbranchial septa of the gills. Here there are no placoid scales and the epidermis is seemingly easy to puncture. *P. cornutus* has no adhesion pads and uses its large, hooked, and pointed second antennae as its primary means of attachment by wrapping them deep into the interbranchial septum. This typically illicits a proliferative tissue reaction by the host which often partially overgrows the anterior portion of the copepod's cephalothorax and probably further assists securement. *Gangliopus pyriformis*, yet another pandarid, attaches directly to the gill filament's delicate secondary lamellae (respiratory surfaces). With no apparent need for adhesion pads, *Gangliopus* has none (males do, however, these are probably associated with some reproductive function). Like *Phyllothyreus*, *G. pyriformis* uses its powerfully hooked second antennae to secure its purchase. *Kroyeria carchariaeglauci* is a small tubularly shaped copepod which lives in the excurrent water channels between gill filaments. Both males and females of this species are proficient swimmers and when the gills are freshly dissected they can be seen scurrying along these water courses, periodically browsing between the secondary lamellae. The cephalotorax of *Kroyeria* species is equipped laterally

Table 3. *Host specificity indices* for some species of shark infesting copepods collected in the western North Atlantic.*

Copepod	**Si(density)**	**Si(freq.)**	**Si(combined)**
Euryphoridae			
Alebion carchariae	0.95	0.81	0.88
A. crassus	1.00	1.00	1.00
A. lobatus	0.86	0.89	0.88
Pandaridae			
Pandarus cranchii	0.58	0.87	0.73
P. floridanus	0.86	0.61	0.74
P. satyrus	1.00	1.00	1.00
P. sinuatus	0.87	0.85	0.86
P. smithii	0.80	0.68	0.74
P. zygaenae	1.00	1.00	1.00
Dinemoura discrepans	1.00	1.00	1.00
D. latifolia	0.77	0.77	0.77
D. producta	1.00	1.00	1.00
Echthrogaleus coleoptratus	0.96	0.82	0.89
Gangliopus pyriformis	1.00	1.00	1.00
Nessipus orientalis	1.00	1.00	1.00
N. tigris	1.00	1.00	1.00
Pagina tunica	1.00	1.00	1.00
Perissopus dentatus	0.78	0.76	0.77
Phyllothereus cornutus	0.96	0.85	0.91
Dichelesthiidae			
Anthosoma crassum	1.00	1.00	1.00

*Calculated according to Rohde (1980).

with two postero-dorsally projecting stylets which possibly help maintain the copepod in its tunnel-like environment through which respiratory water continually passes. Ventrally, both the claw shaped second antennae and the scythe shaped maxillipeds are used to hold on to the rather heterogeneous range of substrates provided by the combined habitats of water channels and interlamellar spaces. Nemesis species typically attach to tissues surrounding the efferent arterioles of the gill filaments. Very large, robust maxillipeds are used to encircle these tissues by hugging and piercing them. The second antennae are used in similar fashion as a secondary means of attachment, and as noted for Phyllothyreus, induced host tissue proliferations appear to futher secure Nemesis individuals by filling the gaps between the host substrate and the parasites grasping appendages.

Therefore, it appears easily demonstrable that while many species of copepods infest the gills of sharks most seem adapted to particular branchial niches. Furthermore, the ability to realize these niches seems to be reflected in the general habitus and mechanical design of various grasping appendages. Given the heterogeneous nature of the branchial region this is not surprising, however, what can be said about the seemingly more homogeneous substrate presented by the general body surface of sharks?

If we examine the distribution of Echthrogaleus coleoptratus on the body surface of its preferred host the blue shark (fig. 3), we find 74 percent of these copepods attached on and about the pelvic fins (including the claspers of males). Given the small area this preferred region represents relative to the entire body surface (fig. 3), this site selectivity certainly is more pronounced than incidence percentages suggest. Males of this species are capable of movement over the host, however like other members of the Pandaridae, adult females appear to be relatively stationary. The location of these parasites at particular body sites may offer reproductive advantages by increasing the likelihood of successful matings.

We are only beginning to realize the high degree of inter- and intraspecific variation (size and shape, relative density, and polarity) exhibited by placoid scales of sharks, and it is currently believed that these tiny dermal elements play a very important hydrodynamic role in the lives of these fishes (Reif & Goto, 1979; Reif, 1982; Reif & Dinkelacker, 1982). Given that many species of copepods infesting the general body surface of sharks tend to exhibit some degree of site selectivity, as exemplified here by E. coleoptratus and as noted elsewhere (Benz, 1981) for Pandarus satyrus, perhaps future investigations examining the actual mechanisms of copepod attachment will uncover evidence correlating the aforementioned variable qualities of placoid scales with the types of grasping devices possessed by copepods. While such investigations themselves will not explain coevolution dynamics of sharks and copepods, they may give us some of the whys and wherefores concerning the spatial distributions we observe in the field today.

ACKNOWLEDGEMENTS

I thank those involved with the many New England shark fishing tournaments which have offered me so many sampling opportunities over the years; and the scientists, officers and crew of the R/V WIECZNO (Morski Instytut Rybacki, Gdynia, Poland) for their diligent assistance on 3 cruises. Sincerest thanks are extended to J.G. Casey, H.W. Pratt, C.E. Stillwell and others involved with the National Marine Fisheries Service Cooperative Shark Tagging Program for arranging my participation at fishing tournaments and upon research cruises, assistance in the field, and extending to me their most valued friendship. F.E. Carey (Woods Hole Oceanographic Inst.) was kind in remembering me while at sea with some nifty copepods, L.R. Penner (Univ. Connecticut) as usual provided space and facilities for studying collections, and my wife, J.M. Benz, spent hundreds of hours in the field recording my data while I plucked and picked my way toward my sampling goals.

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Appendix I.

List of copepods collected from sharks in the western North Atlantic. Number in parentheses after shark name refers to number of sharks examined. Number in parentheses after copepod name indicates number of collections.

- white shark (6)
  - Anthosoma crassum (1)
  - Nemesis lamna (1)
  - Dinemoura latifolia (4)
  - Nessipus orientalis (1)
  - Pandarus cranchii (2)
  - P. floridanus (2)
  - P. smithii (5)

- shortfin mako (48)
  - Nemesis lamna (6)
  - Dinemoura latifolia (38)
  - Gangliopus pyriformis (1)
  - Pandarus cranchii (12)
  - P. sinuatus (1)
  - P. smithii (15)
  - Phyllothyreus cornutus (4)

- longfin mako (1)
  - Pandarus cranchii (1)

- porbeagle (1)*
  - Dinemoura producta (1)

- thresher shark (4)
  - Nemesis robusta (4)
  - Pandarus floridanus (1)

- bigeye thresher (2)
  - Bariaka alopiae (2)
  - Dinemoura discrepans (2)
  - Pandarus smithii (1)
  - Pagina tunica (2)

- blue shark (59)
  - Kroyeria carchariaeglauci (8)
  - Kroeyerina sp. (8)
  - Eudactylina sp. (1)
  - Caligus productus (1)**
  - Echthrogaleus coleoptratus (35)
  - Gangliopus pyriformis (2)
  - Pandarus satyrus (25)
  - P. cranchii (2)
  - P. smithii (3)
  - Phyllothyreus cornutus (11)

- night shark (12)
  - Alebion lobatus (1)
  - Echthrogaleus coleoptratus (1)
  - Pandarus smithii (12)
  - Opimia sp. (1)

- sandbar shark (7)
  - Pandarus sinuatus (3)
  - P. smithii (4)
  - Perissopus dentatus (2)

- bignose shark (8)
  - Nemesis sp. (8)
  - Alebion carchariae (1)
  - A. lobatus (2)
  - Pandarus sinuatus (1)
  - P. smithii (8)
  - Perissopus dentatus (1)

- dusky shark (1)
  - Pandarus chranchii (1)
  - P. smithii (1)

- silky shark (8)
  - Pandarus floridanus (3)
  - P. smithii (5)

- tiger shark (3)
  - Alebion carchariae (1)
  - Nessipus tigris (1)
  - Pandarus cranchii (1)
  - P. floridanus (1)
  - P. smithii (3)

- scalloped hammerhead (18)
  - Alebion carchariae (1)
  - A. crassus (15)
  - Echthrogaleus coleoptratus (1)
  - Pandarus smithii (10)
  - P. zygaenae (3)

- smooth dogfish (2)
  - Caligus chelifer (1)**
  - Perissopus dentatus (1)

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* This is the only collection taken outside of the study area noted in Fig. 1. It was taken in the Penobscot Gulf.

** Caligus species are not considered parasites of sharks, and the 2 collections listed here are considered significant only because they are curious records.

INDIVIDUAL AND COMBINED EFFECTS OF SALINITY AND TEMPERATURE ON THE CALANOID COPEPOD *PARACALANUS ACULEATUS* GIESBRECHT.

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Abstract: Individual and combined effects of salinity and temperature on the survival were investigated in the laboratory on the calanoid copepod *Paracalanus aculeatus* Giesbrecht. The animals tolerated salinities from full strength seawater (35°/oo) down to 37% seawater when subjected to sudden exposure, but gradual acclimation increased the animal's ability to tolerate even 20% seawater. Temperatures tolerated by the animals ranged from 6°C to 33°C. Optimal conditions for survival occurred at salinities 100% to 60% seawater and temperatures 25°C to 32°C. Experimental results are compared with field observations and a relationship between the salinity and temperature of seawater and occurrence of this copepod in large number in Indian coastal waters in the pre-monsoon period (April - June) is discussed.

INTRODUCTION

Paracalanus aculeatus Giesbrecht is a common calanoid copepod of Indian coastal waters. It occurs in inshore waters of both the east and west coast of India, as well as in the backwaters and estuaries (George, 1953; Krishnaswamy, 1953a,b; George, 1958; Kartha, 1959; Kasturirangan, 1963; Goswami and Selvakumar, 1977; Goswami et al., 1977; Menon, 1977; Goswami, 1979; Madhupratap, 1979; Nair and Thampy, 1980). *P. aculeatus* is a typical marine form with a very wide distribution in most of the oceans of the world (Krishnaswamy, 1953a). Kasturirangan (1963) is of the opinion that the two species of *Paracalanus* (*P. aculeatus* and *P. parvus*) share with the species of two other calanoid copepods, *Acartia* and *Oithona* the distinction of being the 'commonest' copepod of inshore waters of the Indian coasts occurring almost throughout the year. However, peak periods of occurrence of *P. aculeatus* have been correlated with the periods of high salinity by some (George, 1953; George, 1958; Madhupratap, 1979; Nair and Thampy, 1980).

Several studies on food and feeding habits of various species of marine and estuarine pelagic fishes and prawns have shown that the copepods form a very important food item (Bal and Joshi, 1956; Venkatraman, 1956, 1961; Dhulkhed, 1964; Mohamed, 1970; George, 1970a,b,c; Rao, 1970). The copepod *Paracalanus* has been found to constitute an important item of diet in inshore fishes such as *Thrissocles mystax*, *Anchoviella tri*, *Caranx* (*Selar*) *kalla* and *Leiognathus insidiator* (Venkatraman, 1956, 1961). *P. aculeatus* is therefore expected to play a very significant role in the food chains of Indian coastal waters, backwaters and estuaries.

P. aculeatus occurs in large number during the pre-monsoon period (March-May) in Bombay coastal waters (west coast of India). It also occurs during other seasons except the monsoon period (June-August) but in less number. Salinity has been considered as a major factor controlling the distribution of *P. aculeatus* in Indian coastal waters (Madhupratap, 1979).

Salinity plays a very significant role particularly in coastal waters of tropical regions like India, since heavy rainfall brings about considerable dilution of seawater. According to Kinne (1963) animals living in coastal, littoral and estuarine waters may encounter death from low salinity as such waters are often subjected to considerable salinity variations due to dilutions especially during heavy rains. Tolerance of copepods to change in water temperature is another important consideration. Temperature can broaden, narrow or shift the salinity range of an animal and salinity can also modify the effects of temperature accordingly (Kinne, 1963). A complex correlation therefore exists between the biological effects of salinity and temperature. The present investigation was therefore carried out to find out effects of changes in salinity and water temperature individually and in combination on survival of P. aculeatus. On establishing the tolerance capacity of the animals to salinity and temperature, the experimental results were compared with field observations with a view to find out the effects of salinity and water temperature on the distribution of P. aculeatus in Indian coastal waters.

MATERIALS AND METHODS

P. aculeatus was collected from a shallow bay in the vicinity of the Taraporevala Marine Biological Research Station, Bombay, India and from a fixed station, located about 3 miles off the Bombay coast. Animals were captured with a plankton net made from bolting silk (No. 10) having a 13-cm-long cylindrical canvas and 71-cm-long conical silk portion. Animals were immediately sorted and packed in polythene bags containing 10 litres of seawater and transported to the laboratory. Animals were maintained in seawater ($35^{o}/oo$ salinity) taken from the Taraporevala Aquarium and at ambient room temperature ($22^{o}C$-$32^{o}C$ depending on the season) which was always very close to field temperature. Animals were used for experimental studies after maintaining them for about 24 hours in the laboratory. Seawater required for experiments was taken from the circulatory system of the Taraporevala Aquarium. This seawater having $35^{o}/oo$ salinity has been taken as 100% seawater. Dilutions of seawater were made by adding distilled water. Animals were fed with freshly hatched nauplii of Artemia salina. Experiments were conducted for 120 hours except salinity acclimation experiments, which lasted for longer periods. Survival time for individual specimens were recorded to obtain % survival. Dead specimens were removed at regular intervals. All experiments were replicated at least twice and mean survival periods were calculated.

Those salinities and temperatures in which at least 50% of the animals survived at the end of 24 hours of exposure, have been considered to be within the tolerance range and the rest as lethal. Dilutions were usually made in steps of 10% (i.e. 90, 80, 70, 60% etc.). Each temperature usually differed from the immediately higher or lower temperatures by $3^{o}C$. In each experiment, 200ml of water and 20 animals were used and the water was changed daily.

Salinity tolerance experiments were conducted at ambient room temperature. Initially, the salinity tolerance range was observed by exposing the animals to salinities from 0 to 100% seawater in increments of 10%. Further experiments were conducted in steps of 5,3 and 1% seawater to determine very precisely the lethal salinity of the copepod.

Experiments on salinity acclimation were designed to determine gain in salinity tolerance. Animals were acclimated by two procedures to find out the effect of rapid or gradual change in salinity.

For the rapid salinity acclimation experiments, eight sets of experiments were designed each time. Batches of copepods acclimated separately in different dilutions for 24 hours were then transferred to lethal salinity and dilutions below lethal salinity. The % survival was recorded in all experimental salinities at the end of 24 hours. For the gradual salinity acclimation experiments, animals were transferred to lethal salinity and salinities below lethal after they were acclimated stepwise from 100% to 20% seawater.

Experiments on temperature tolerance were conducted in glass aquaria of 30 X 23 X 23 cm with a 100 W immersion heater controlled by thermostats with a sensitivity of $\pm$ 0.5°C. In experiments below ambient room temperature refrigerated aquaria were used. Conical flasks containing animals were partially immersed in aquaria and water temperature in the flasks noted.

Initially the temperature tolerance range was determined by exposing the animals to various temperatures above and below ambient room temperature usually in steps of 3°C. Further experiments were conducted in steps of 1°C between the acute and lethal temperatures to more precisely define the upper and lower temperatures.

For experiments on the combined effects of temperature and salinity, various combinations of salinity and temperature were made within the tolerance range of the animals. Each combination differed by 10% seawater and 3°C, except for determination of the effect of salinity on lethal temperature and of temperature on lethal salinity. In these cases combinations differed by 2-3% seawater and 1°C. Details of the methods have been described elsewhere (Bhattacharya and Kewalramani, 1973, 1982).

RESULTS

Animals exhibited best survival in full strength seawater. There was a gradual decrease in survival as the salinity decreased down to 40% seawater (Fig. 1). At the lower end of the salinity range, % survival was poor at concentrations below 37%, and 35% seawater was found to be lethal.

The experiments on salinity acclimation indicated that animals can tolerate salinities below 37% seawater if they are acclimated in various salinities either directly or gradually. However, the gain in salinity tolerance was found to be related to the acclimation salinity and the nature of acclimation.

In the experiments on direct acclimation (Table 1), it was observed that the animals could tolerate 35% seawater after they were acclimated in 60% seawater for 24 hours. But a considerable gain in salinity tolerance was noticed after the animals were acclimated in 50% seawater for 24 hours. There was no mortality in 37% seawater after they were acclimated in 40% seawater. Lethal salinity was reduced to 20% seawater when the copepods were acclimated directly in 40% seawater for 24 hours. The copepods however could not tolerate 20% seawater even when they were acclimated directly in 37% seawater for 24 hours.

In the experiments on gradual salinity acclimation (Table 2), the first indication of any change in lethal salinity was observed after the copepods were gradually acclimated down to 50% seawater. Animals could tolerate 35% seawater at this stage. Percent survival increased to 100% after the copepods were gradually acclimated down to 50% seawater. They could tolerate 30% seawater when acclimated down to 50% seawater and even 20% seawater when gradually acclimated down to 37% seawater. However, the copepods could not tolerate 10% seawater even after gradual acclimation down to 20% seawater.

Table I. *Effect of direct salinity acclimation on salinity tolerance of P. aculeatus. Data represent the % survival of animals exposed to lethal salinity (determined from acute tolerance experiments) and salinities below lethal after 24 hours exposure to various salinities from 100% to 37% seawater.*

Acclimation salinity	% survival			
	Lethal salinity	Salinities below lethal		
(% seawater)	35%	30%	20%	10%
100	20	0	0	0
90	25	0	0	0
80	30	0	0	0
70	40	0	0	0
60	50	20	0	0
50	90	40	0	0
40	100	60	20	0
37	100	70	40	0

Table II. *Effect of gradual salinity acclimation on salinity tolerance of P. aculeatus. Data represent % survival of animals exposed to lethal salinity (determined from acute tolerance experiments) and salinities below lethal for 24 hours after gradual acclimation for 24 hours to decreasing salinities from 100% seawater. Dashes indicate no experiments run at that combination.*

Acclimation salinity (% seawater)											% survival			
											Lethal salinity	Salinities below lethal		
											35%	30%	20%	10%
100	90	80	70	60	50	40	37	35	30	20				
*											20	0	0	0
*	*										20	0	0	0
*	*	*									25	0	0	0
*	*	*	*								30	0	0	0
*	*	*	*	*							70	60	0	0
*	*	*	*	*	*						100	70	0	0
*	*	*	*	*	*	*					100	80	50	0
*	*	*	*	*	*	*	*				-	100	60	0
*	*	*	*	*	*	*	*	*			-	-	70	0
*	*	*	*	*	*	*	*	*	*		-	-	-	0
*	*	*	*	*	*	*	*	*	*	*	-	-	-	0

* Animals were exposed to each of these salinities for 24 hours in sequence.

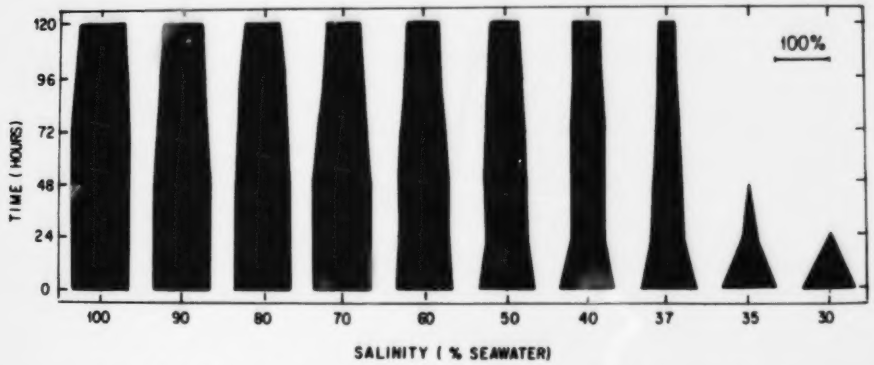

Figure 1. *Percent survival of* P. aculeatus *Giesbrecht exposed to different salinities (% seawater) for 120 hours.*

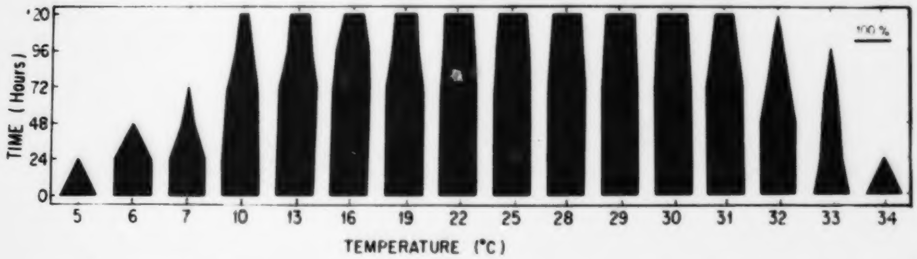

Figure 2. *Percent survival of* P. aculeatus *Giesbrecht exposed to different water temperatures (°C) for 120 hours.*

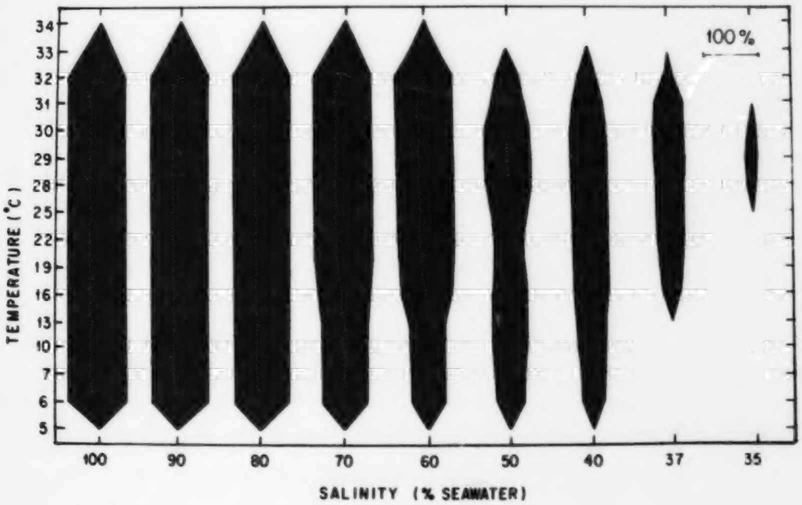

Figure 3. *Percent survival of* P. aculeatus *Giesbrecht exposed to different combinations of temperature and salinity for 24 hours. Note that the temperature axis is not continuous.*

Experiments on temperature tolerance indicated that animals could tolerate temperatures up to 33°C at the upper limit and down to 6°C at the lower limit (Fig. 2). The upper and lower lethal temperatures were found to be 34°C and 5°C, respectively. Animals exhibited best survival in 28°C-30°C. There was only 20% mortality in these temperatures at the end of 120 hours. Percent survival decreased with increase in exposure time in all temperatures above and below this range. Animals exhibited a very sudden change in survival pattern at the lower limit of temperature range. Percent survival in 5°C was found to be 0% at the end of 24 hours, whereas in 6°C it was 100%.

Experiments on the combined effects of salinity and temperature were carried out for 24 hours to determine the effect of temperature on lethal salinity, as well as the effect of salinity on lethal temperature. In these studies, % survival also served as an indicator of tolerance of animals to various temperature-salinity combinations.

The widest range of salinity tolerated by the copepod was from 100% to 37% seawater at temperatures ranging from 22°C to 31°C. The lethal salinity was slightly affected by any temperature change at the lower limit. The lethal salinity rose to 40% in 7°C. However at the upper limit the lethal salinity rose to 60% seawater in 33°C. The lower lethal temperatures were only slightly affected by salinity (Fig. 3).

DISCUSSION

Experiments on salinity tolerance indicate that P. aculeatus can tolerate salinities in the range of 100% - 37% seawater when subjected to sudden exposure. However, mortality rate increased sharply at salinities below 37% seawater. Animals exhibited best survival in full strength seawater and there was a gradual decrease in % survival with decrease in salinity.

Salinity acclimation experiments reveal that the animals can tolerate salinities below 37% seawater if acclimatization occurs. The animals can tolerate dilutions down to 30% seawater if there is a rapid change in salinity. They can tolerate salinity as low as 20% seawater if slow acclimatization occurs. The salinity of Bombay coastal waters decreases to about 13°/oo in the monsoon (Gogate, 1960). This change in salinity may be very rapid or gradual depending on the intensity of rainfall. The present laboratory investigations suggest that the salinity of Bombay coastal waters in the monsoon is not very favourable to the animals. Although the animals have the capacity to tolerate dilution down to 37°/o seawater and below, depending on the acclimatization, high mortality in low salinities with increase in exposure time indicates that they may not occur in inshore waters during the monsoon period. Salinity of backwaters and estuaries on both coasts of India decreases greatly in the monsoon. George (1958) observed that salinity of Cochin backwaters (south west coast of India) declined to as low as 1.2°/oo in the monsoon period (August to October). It can therefore be concluded from the present laboratory experiments that the salinity of the backwaters and estuaries in the monsoon period is not at all favourable to the animal. P. aculeatus has been included amongst the group of copepods which are predominantly high saline by Madhupratap (1979). Goswami and Selvakumar (1977) considered this copepod as a marine-brackish (orthosteno-euryhaline) animal. According to Menon (1977) P. aculeatus is an euryhaline species. Krishnaswamy (1953) considered it as a typical marine form. The present laboratory investigations suggest that the animal may be considered as an euryhaline form. It has the capacity to enter estuaries and backwaters but high mortality in low salinities with increase in exposure time indicates its inability to live permanently in these environments. Moreover, daily repeated salinity changes in an estuary may have a cumulative effect and restrict the animals to salinities higher than those shown in the laboratory (Bassindale, 1943).

Temperature tolerance experiments have shown that any change of temperature in the range of 6°C to 33°C is within the tolerance limit of the copepod. However, high mortality at temperatures above 30°C and below 28°C with increase in exposure time indicates that temperature may act as an important factor in the distribution of P. aculeatus. Temperature in Indian coastal waters, estuaries and backwaters varies between 22°C and 32°C (Prasad, 1958; George, 1958; Bhattacharya, 1973; Nair and Thampy, 1980). P. aculeatus exhibited best survival in a very narrow range of temperature (28°C-30°C). The experiments therefore suggest that at the higher limit, the copepod will be affected by temperatures slightly higher than those to which they are accustomed. This finding, therefore, supports the suggestions of Kinne (1963) that at the upper extreme, many organisms are killed by temperatures slightly higher than those to which they are accustomed.

Observations made on the combined effects of salinity and temperature suggest that there was no change in lethal salinity in the range 22°C to 31°C. However, there was a considerable decrease in the salinity tolerance range above 31°C. Reduced salinity seems to have little effect on the lower lethal temperatures of the animal. But upper lethal temperatures were reduced in lower salinities.

It may therefore be concluded that P. aculeatus is an euryhaline form. But it can tolerate a wide range of salinity (100%-37% seawater) for a short period. This copepod has the capacity to enter estuaries and backwaters but high mortality in diluted seawater with increase in exposure time suggests its inability to live permanently in these environments. P. aculeatus seems to be better adapted for survival in high salinity and high temperature conditions. Madhupratap (1979) observed that the maximum salinity (°/oo) range and optimum salinity for P. aculeatus were 13.5-34.5°/oo and 25.5-34.5°/oo, respectively. According to Thampy and Nair (1980) it occurs during the pre-monsoon period when the salinity and the temperature of Cochin backwaters vary between 29-30°/oo and 29°C-30.5°C, respectively. George (1953) noticed that P. aculeatus were more common during the summer when the salinity and the temperature were high. Present laboratory investigations therefore support all the previous field observations. The experiments also suggest that the optimal conditions for survival in the case of P. aculeatus occur at salinities 100% to 60% seawater and temperatures in the range of 25°C to 32°C.

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COMPARATIVE NOTES ON THE DEVELOPMENT OF TWO SPECIES OF BRYOCYCLOPS (COPEPODA, CYCLOPOIDA)

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Two species of Bryocyclops, namely Bryocyclops absalomi Por, 1981 and Bryocyclops caroli (Bjornberg, 1985) were reared under laboratory conditions. The first species inhabits carstic caves in Israel and the second, epigeic plant litter in Sao Paulo, Brazil. The detailed description of the naupliar and copepodid stages of the two species and a comparative discussion of them form the subject of a separate paper (Bjoernberg, in preparation).

Here a few comparative considerations on the development rate of these species are being made, especially with reference to the results and discussion made by Lescher-Moutoué (1973). This author reared a number of subterranean (hypogeic) cyclopoid species at 11.5°C and compared the duration of a complete developement cycle in these species, with that of surface-living (epigeic) cyclopoids. The conclusion reached by Lescher-Moutoué points to the fact that the development rate of the hypogeic species is much slower than that of the epigeic ones.

Bryocyclops, a moss and litter living and facultative subterranean genus, is considered to be the parental genus of the subterranean Speocyclops (Menzel, 1928; Kiefer, 1928; Lindberg, 1954; Rylov, 1948; Monchenko, 1972). Therefore, we considered that a comparison of the development rate of two species of the first mentioned genus with that of other cyclopoids may be of interest. Both B. absalomi and B. caroli were kept at a temperature of 20-22°C, i.e. corresponding to their natural environment temperature. The first species was kept at a pH of 6-7 and the second at pH 5. The comparative data are presented in Table I.

We reach the conclusion that Bryocyclops does not show the retardation in development which seems to characterize the subterranean cyclopoids but rather has a rapid development characterizing the surface-living species. This finding seemingly confirms the assumption that Bryocyclops absalomi is an opportunistic settler of the cave environment in Israel, penetrating from a wet environment at the surface (Por, 1981).

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Table 1: *Developmental rates of hypogeic and epigeic cyclopoids*

Species	Reference	Duration (in days) of			Temperature
		egg eclosion	post-embr.devel.	total develop.	(°C)
Hypogeic					
Speocyclops gallicus	Lescher-Moutoué, 1973	17	87	105	11.5
Speocyclops racovitzai	" " "	13-14	111	125	11.5
Graeteriella unisetigera	" " "	12	93	105	11.5
Acanthocyclops stammeri westphalicus	" " "	14-15			11.5
Epigeic					
Acanthocyclops viridis	Walter, 1922	5			12
	" "		30		29
	" "		120		2
Mesocyclops leuckarti	Gras and Saint Jean, 1969	2			22
	Einsle, 1968	9-10			11
Eucyclops serrulatus	Lescher-Moutoué, 1973	8			11.5
	Rylov, 1948		14		10
Bryocyclops absalomi	original	3-4	12-14	15-18	22
Bryocyclops caroli	original	3-4	12-24	15-28	22

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THE REJECTED NAUPLIUS : A COMMENTARY.

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ABSTRACT: Modern classifications of copepods have not considered the naupliar stages. Based on these, subfamilies should be raised to family rank and families belonging to the same superfamily should be separated into different superfamilies.

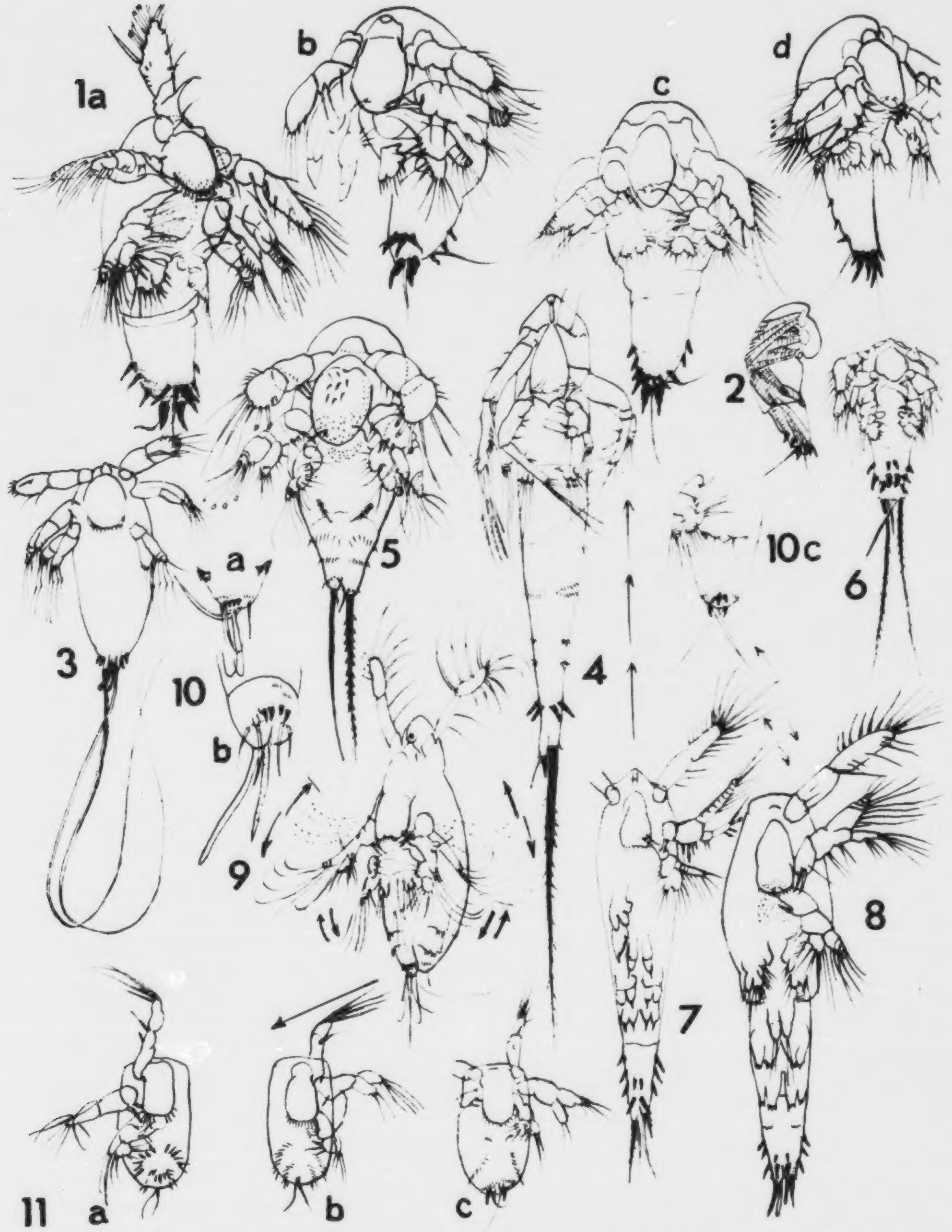
Plesiomorphic and apomorphic characters are observed in the nauplii. Cyclopoid and calanoid nauplii living in the plankton are more plesiomorphic, and harpacticoid nauplii are more apomorphic. Based on these considerations the use of some nauplii, when possible, is recommended in the classification of copepods.

Nauplii have not been considered for taxonomical studies in copepods up to now. Some of the oldest classifications, Giesbrecht's (1892) for example, did not consider the nauplii because they were unknown for most species. From then up to now many nauplii, were identified by rearing eggs from known females, or by maintaining the sixth nauplius stage through metamorphosis to the first identifiable copepodid stage (see Bjornberg, 1972; Sazhina, 1982). There are now many species with known developmental stages. Thus, it is to be lamented that for the last attempts to systematize the copepods (such as Andronov's, 1974; Bowman and Abele's, 1982) the nauplii were not examined. The reasons for this are probably the three following: 1) there are still unknown nauplii for whole copepod families; 2) some nauplii are lecitotrophic, and the great quantity of yolk masks their generic and specific characters; 3) environmental pressures act onto each stage of development of the species from egg to adult altering the morphology of the various stages.

None of these arguments, however, should be used as reasons for rejecting the characteristics of the known nauplii in the attempts to organize the adult specimens into families and superfamilies (see Williamson, 1982) because the naupliar features are just as important as the adult's.

The result of ignoring these characteristics is the inclusion in the same superfamily of families in which nauplii are totally different and of the placing into different superfamilies of genera whose nauplii are practically identical. The best known nauplius among the Calanoida is the comma-like or hook-like nauplius (type I of Sazhina, 1982) which being top heavy moves about by turning successive somersaults (Fig. 1). It has two posterior balancers or feelers, 3 lateral spines on each side, 2 terminal ones and 4 subterminal spines in stage V, which I consider the most developed of the naupliar stages. It is the nauplius of Calanus, Pseudocalanus, Paracalanus, Microcalanus, Ctenocalanus and Calocalanus. Without the two posterior balancers it is also the nauplius of the Metridinidae. The fact that this same nauplius (varying only in size and in the number of some setae in the anterior region) (Fig. 1) appeared in so many different genera cannot be attributed to as many convergences, because even the muscle system of these nauplii is the same (Fig. 2).

In the Bowman and Abele (1982) system the superfamily Clausocalanoidea includes the Clausocalanidae and the Euchaetidae with quite different nauplii (Fig. 1b and 3). The same happens with the superfamily Centropagoidea in which Pontellidae, Pseudodiaptomidae, Temoridae and Acartiidae are all placed together, though having the most diverse nauplii (Figs. 4, 5, 6, 11). The inclusion of the



Figures 1-11: *1: Hook-like Nauplius: **a** - of Calanoides carinatus, stage V, 0.45 mm long; **b** - of Clausocalanus furcatus, stage V, 0.25 mm; **c** - of Paracalanus aculeatus, stage V, 0.22 mm long; **d** - of Calocalanus pavo, stage IV, 0.17 mm long. 2: Muscle system of hook-like nauplius (Paracalanus sp.). 3: Nauplius of Euchaeta marina. 4: Nauplius V of Pontellopsis brevis, 1.45 mm long, balancer included, ventral view. 5: Nauplius III of Pseudodiaptomus acutus, 0.22 mm. 6: Nauplius V of Temora stylifera, 0.23 mm. 7: Nauplius IV of Rhincalanus sp., 1 mm. 8: Nauplius VI of Eucalanus elongatus, 1 mm (after Johnson, 1937). 9: Nauplius VI of Eucalanus pileatus, 1 mm long. 10: Posterior ventral region of nauplius: **a** - Eucalanus pileatus; **b** - Eucalanus (attentuatus) langae; **c** - Centropages furcatus. 11: Ventral view of nauplii stage II of Acartia: **a** - A. clausi; **b** - A. tonsa; **c** - A. danae (**a** and **b** after Conover, 1956; **c** after Bjornberg, 1972.)*

families Calanidae, Calocalanidae and Paracalanidae in the same superfamily (Megacalanoidea) merits approval because they have the same type of nauplius, although the calocalanids' is a slightly longer nauplius and therefore has the capacity of moving for short distances without somersaulting.

The contrary happens with the superfamily Eucalanoidea created for only one family, the Eucalanidae. The genera *Rhincalanus*, *Eucalanus*, *Paraeucalanus* and *Subeucalanus* (these two last genera recently added by Geletin, 1976) composed the family. Fleminger (1973) studied the integumental organs (pores and sensillae) of the genus *Eucalanus sensu latu*, dividing it into 4 groups of species: 1) *elongatus*, 2) *attenuatus*, 3) *subtenuis* and 4) *pileatus*. Unfortunately the integumental organs of the genus *Rhincalanus* were not studied. These have a nauplius which is almost the same as the one of the *Eucalanus elongatus*, excepting as to the symmetry (Gibbons, 1936). These nauplii could have originated from the hook-like nauplii by a considerable lengthening of the posterior region. By flapping its appendages, locomotion by successive impulses results. Their setation is the same as that of the hook-like nauplii (Fig. 7, 8). The other species of the genus *Eucalanus*, *E. pileatus* and *E. crassus*, which belong respectively to the Fleminger groups *pileatus* and *subtenuis* have quite different nauplii which look almost alike. Their setation is very reduced when compared to the *E. elongatus* nauplius, they are also far more asymmetrical, and their locomotion is also quite different. They glide through the water in an almost vertical position, maintaining their antennules stretched out rigidly above the frontal region, like frontal keels. Locomotion is by vibration of the antennae and mandibles. With a strong posterior asymmetry in their two last stages of naupliar development, they show 4 minute subterminal spines in one of the two posterior lobes, and two terminal long balancer setae or feelers besides some sensory setae (Fig. 9). The *E. attenuatus sensu latu* nauplius is also asymmetrical, and looks like the one of *E. pileatus* (see Fig. 10), but, it is more elongated and in the sixth stage it has more posterior setae. Fleminger (1973) created 2 new species for the populations *E. attenuatus*-like with pores and sensillae differing from the typical one. Thus, *E. sewelli* is the species of the *E. attenuatus* group which occurs in the tropical and subtropical Atlantic, and its nauplius is the one described for the *E. attenuatus* from Curacao (Björnberg, 1967). The other nauplius found off Chile and very much like this one, but with less subterminal spines belongs probably to the other species of the *attenuatus* group, *E. langae*. Summarizing, there are 2 types of nauplii, quite different, even in their locomotion in one only family and superfamily - the nauplius derivable from the hook-like calanid nauplius, and, the other, more like the *Centropages* nauplius.

Geletin (1976) created two new subfamilies inside the Eucalanidae, the Rhincalaninae, with the only genus *Rhincalanus*; the Subeucalaninae, with the new genus *Subeucalanus* and the only species *S. subtenuis*. Giesbrecht's (1892) Eucalaninae should contain the genera *Eucalanus* (with the type species *E. elongatus*) and the new genus (Geletin, 1976) *Paraeucalanus*, with the type species *P. attenuatus* (Geletin, op. cit.). Based on the nauplii we agree with Geletin in creating the subfamilies Rhincalaninae and Eucalaninae, but, we can not approve the inclusion of the genus *Paraeucalanus* in the Eucalaninae. The subfamily Subeucalaninae could remain valid if elevated to the category of family, Subeucalanidae Geletin 1976, containing the genera *Paraeucalanus* Geletin 1976, with the type species *P. attenuatus* (Dana, 1849), and, *Subeucalanus* Geletin 1976, with the type species *S. subtenuis* (Giesbrecht, 1888). The superfamily Eucalanoidea Giesbrecht 1892 should thus contain the family Eucalanidae Giesbrecht, 1892 with two subfamilies Rhincalaninae Geletin, 1976 and Eucalaninae Giesbrecht, 1892. The family Subeucalanidae Geletin 1976, redefined to contain the two genera *Paraeucalanus* and *Subeucalanus* should be placed in the superfamily Centropagoidea Giesbrecht, 1892, because the nauplii of *Centropages* and of *E. attenuatus*, *E. pileatus* and *E. crassus* are very similar.

Amongst the known nauplii, those which suffered greater changes because of adaptations to the most varied environments in which they live, are the Harpacticoida. In these nauplii the primitive characters are the plumose setae or the simple setae and the derived characters are the numerous hooks, pincers, spines and other adaptations to the benthonic niches. The flattened oval form of the body is also probably primitive.

In the Calanoida and Cyclopoida the nauplii are generally planktonic and without such modified features as those observed in the Harpacticoida. The oval shape of the body is also considered primitive. The cylindrical antennules and antennae, also. The flattening out of these appendages, the lengthening of the posterior part of the body of the nauplius, the transformation of the setae into spines or their increase in size, their change into sensory organs, or balancers, movements of types diverging from locomotion by successive impulses are probably apomorphic. A primitive character of the cyclopoid nauplius is undoubtedly the double-jointed endopod of the mandible, which in the other nauplii is composed of one joint. Nauplii which live in the plankton are less modified because the environment in which they live is more homogeneous. Nauplii suffer the pressure of the environment just as any other stage of development, but, being small and less developed they also have less structures on which the environment acts. An adult submits a greater number of characters to speciation processes than the younger stage. It is because of this phenomenon, that von Baer's (1828) law states that the earliest embryonic stages of related organism are identical; distinguishing features are added later as heterogeneity differenciates from homogeneity. Nauplii of copepod species of near kinship are sometimes almost indistinguishable. They differ only in the number of setae, or in size. Compare the nauplii of Acartia f. i. (Fig. 11). If nauplii of near related species are almost identical, it is to be expected that nauplii of related genera do not look different and that this also applies for larvae of related families.

Not to consider nauplii in taxonomical studies is perhaps a great loss of time, especially in the case of Calanoida and Cyclopoida whose naupliar stages show less adaptations to different environments than the Harpacticoida. Ecologically the nauplii are far more important than the adults, because most copepods never reach the copepodid stages, they are eaten while still in their naupliar form.

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FRESHWATER CALANOID COPEPODS OF THE WEST INDIES

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Abstract: Five species in 3 genera of Diaptomidae are known to occur in the West Indies. *Arctodiaptomus asymmetricus* and *Mastigodiaptomus purpureus* are endemic to Cuba. *A. dorsalis*, found in the southern United States from Arizona to Florida, is known from Cuba and Haiti. *Mastigodiaptomus nesus* n. sp. *aff. M. albuquerquensis* (the latter occurring in western North America from Colorado and Utah south to Guatemala) is recorded from 7 islands in the Bahamas from Eleuthera to South Caicos, from Cuba, and from the Cayman Islands. The foregoing species have North American affinities. *Pectenodiaptomus caperatus*, known from Barbuda and Marie Galante, has South American affinities.

Reports of freshwater calanoids in the West Indies are few. The earliest published records are by Marsh (1907), who described *Diaptomus asymmetricus* and *D. purpureus* from Havanna, Cuba. Kiefer (1936) described *Diaptomus proximus* from Laguna Rincón, Haiti. Kiefer's species was synonymized with *Diaptomus dorsalis* Marsh, 1907 by Wilson (1959). Straskraba (1969), in a synopsis of Cuban freshwater crustaceans, listed Marsh's species (as *Acanthodiaptomus asymetricus* (sic) and *Mastigodiaptomus purpureus*) without additional localities. Smith and Fernando (1978) reviewing Cuban freshwater calanoids, added to Marsh's species, listed as *Arctodiaptomus asymmetricus* and *Mastigodiaptomus purpureus*, two species, *Diaptomus dorsalis* (as *Arctodiaptomus dorsalis*), and *Mastigodiaptomus albuquerquensis* (Herrick, 1895), the latter previously recorded from western North America from Colorado and Utah south into Guatemala (Wilson, 1959).

Thus far 4 species of freshwater calanoids had been reported from the West Indies, all from Cuba except the single record from Haiti. The first (and thus far the only) species recorded from the Lesser Antilles was *Notodiaptomus caperatus* Bowman, 1979, from Barbuda. It was later reported from Marie Galante, Guadeloupe, by Dussart (1982) who established the new genus *Pectenodiaptomus* for it.

In 1979 the University of Amsterdam Expeditions to the West Indies collected on Jamaica, Haiti, the Cayman Islands, and 8 islands in the Bahamas. The calanoids in these collections were kindly made available to me by Dr. Jan H. Stock. In addition, I have received Bahamian calanoids from Mr. Douglas J. Barr, who has made extensive collections on the island of San Salvador. All the calanoids in the Stock and Barr collections have been identified as a new species of *Mastigodiaptomus*, similar to *M. albuquerquensis*, but differing from it by the features given in the diagnosis below.

***Mastigodiaptomus nesus*, new species** (Figs. 3-4)

Mastigodiaptomus albuquerquensis. - Smith and Fernando, 1978:2016, figs. 2-4 (non Herrick, 1895). *Diaptomus (Mastigodiaptomus) albuquerquensis*. - Smith and Fernando, 1980:11-12, fig. 4A-C (non Herrick, 1895).

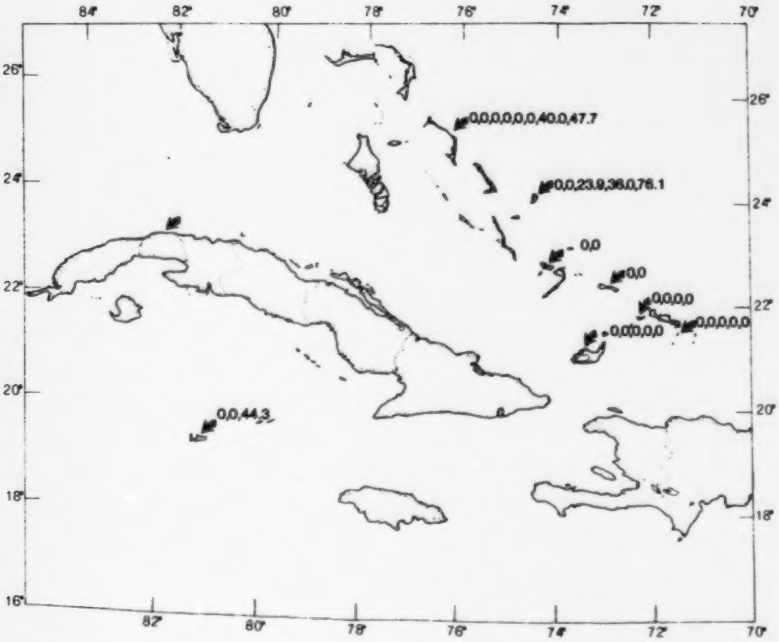
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Figure 1. *Known distribution of* *Mastigodiaptomus nesus. Arrows point to islands where* *M. nesus* *has been collected. Numbers to the right of the arrows indicate the percentages of adult ♀♀ with dorsal processes at different localities on the island.*

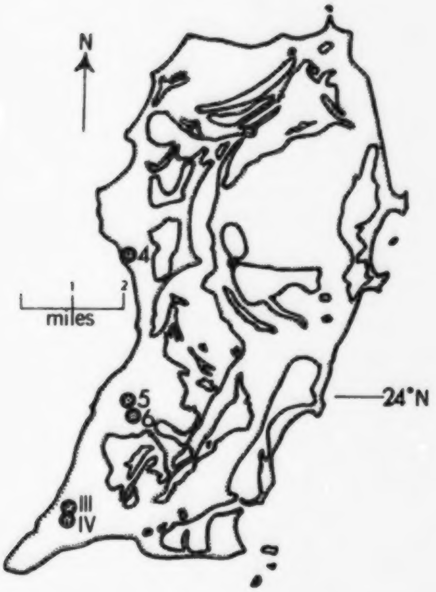
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Figure 2. *San Salvador, showing localities of Ponds 4-6 and Blue Holes III and IV.*

Material. - 1. From the 1979 University of Amsterdam Expedition to the West Indies, led by Jan Stock (Fig. 1). CAYMAN ISLANDS. Grand Cayman: Sta. 79/58, 27 Oct., Water Ground, well, 96♀, 96♂; 79/59, 27 Oct., Birch Tree Hill, well, 3♂, 79/63, Lower Valley, "Melbourne Watler's well", (pool, 4X 2.5 m), 11♀, 6♂. BAHAMA ISLANDS. Eleuthera: 79/98, 8 Nov., Millers, well, 10♀, 14♂, 1 juv.; 79/99, 8 Nov., N side of Bannerman Town, well, 63♀, 72♂; 79/100, 8 Nov., The Village, 2 wells, 2♀, 1♂; 79/101, 8 Nov., Foxhill, well, 2♂; 79/102, 8 Nov., Waterford, well, 2♀, 1♂; 79/108, 8 Nov., S of Savannah, well, 86♀, 50♂, 1 juv.; 79/109, 9 Nov., Upper Boque, well, 10♀, 4♂; 79/111, 9 Nov., The Bluff, well, 1♀, 3♂. Crooked Islands: 79/199, 27 Nov., Cabbage Hill (South), well, 41♀, 12♂; 79/202, 27 Nov. Boats' well, 1♂. Mayaguana: 79/128, 11 Nov., Betsey Bay, cemetery public well, 5♀; 79/129, 11 Nov., Betsey Bay Windpumps, 2 wells, 1♀; Inagua: 79/160, 18 Nov., Salt Pond Hill no. 1, cave pool, 1♀; 79/161, 18 Nov., Salt Pond no. 1, pothole, 38♀, 48♂; 79/162, 18 Nov., Maroon Hill Cave, gours, at entrance of shallow cave, 75♀, 164♂; 79/163, 18 Nov., near Company Beach (off Man of War Bay), well, 1♀, 2♂; 79/165, 18 Nov., Blake's well no. 1, 35♀, 49♂; 79/166, 18 Nov., Blake's well no. 3, 2♀. TURKS AND CAICOS ISLANDS. Providenciales: 79/153, 16 Nov. Five Cays Settlement, well, 79♀, 159♂, 7 juv.; 79/154, 16 Nov., Blue Hills Settlement, near school, well, 102♀, 60♂, 2 juv.; 79/155, 16 Nov., Blue Hills Settlement, John David well, 1♀, 5♂; 79/156, 16 Nov., "The Hole" (Long Bay Hills), cenote-like pit, 1♀, 2♂. South Caicos: 79/145, 14 Nov., Godet Fields wells (3), 120♀, 57♂; 79/146, 15 Nov., Basden's well at Cockburn Harbor, 4♀; 79/147, 15 Nov., Cockburn Harbor, side branch of The Fountain, karst hole, 79♀, 83♂, 5 juv.; 79/148, 15 Nov., Cockburn Harbor, close to The Fountain, karst cleft, 11♀, 12♂; 79/149, 16 Nov., pasture well, east, 112♀, 76♂, 6 juv.

2. - From collections made on San Salvador Island by Douglas J. Barr (Fig. 2). Pond 4, near Cockburn Town, 29 Jan. 1981, depth 0.6 m, water tea-colored, hard substrate with green algae, S = 5 %o, 50+ paratypes, USNM 216168. Pond 5, SW part of island, 30 Jan. 1981, depth ca. 0.5 m, water tea-colored, bottom muddy, S = 10%o, 500+ paratypes, USNM 216167. Pond 6, SE of Pond 5, 30 Jan. 1981, depth 0.3 m, water clear, bottom muddy, S = 4%o, 100+ paratypes, USNM 216171. Blue Hole III (see Hobbs, 1978, fig. 3), 30 May 1984, S = 4%o (Hobbs reported 2%o for Dec. 1977), 50+ paratypes, USNM 216169. Blue Hole IV (see Hobbs, 1978, fig. 3), 5 June 1984, S = 7%o (Hobbs reported 11.2%o for Dec. 1977), 100+ paratypes, USNM 216170.

Types. - Holotype, USNM 216166, 1.52 mm ♀ from Pond 5, San Salvador. The other specimens from the 5 collections made by Barr on San Salvador are paratypes.

Diagnosis. - Length of 10♀♀ from Pond 4, San Salvador, 1.44-1.54 mm, ave. 1.48 mm; prosome: urosome about 2.7. Length of 10♂♂ from Pond 4, 1.30-1.44 mm, ave. 1.34 mm, prosome: urosome about 2.15. Pediger 4 with or without a dorsal process in adult ♀. Very similar in overall appearance to *M. albuquerquensis* (Herrick), but with the following differences:

Mastigodiaptomus nesus	***M. albuquerquensis***
- Dorsal process concave anteriorly (Fig. 3 G,K).	- Dorsal process convex or slightly concave anteriorly (Fig. 3 M, N).
- ♀ genital segment ca. 1.2X as long as wide (Fig. 3A-C)	- ♀ genital segment ca. as wide as long (Fig. 3D)
- ♀ pediger 5 left wing bent anteriad ventral to lower spine (Fig. 3 G, H)	- ♀ pediger left wing without bend below lower spine (Fig. 3I, J).

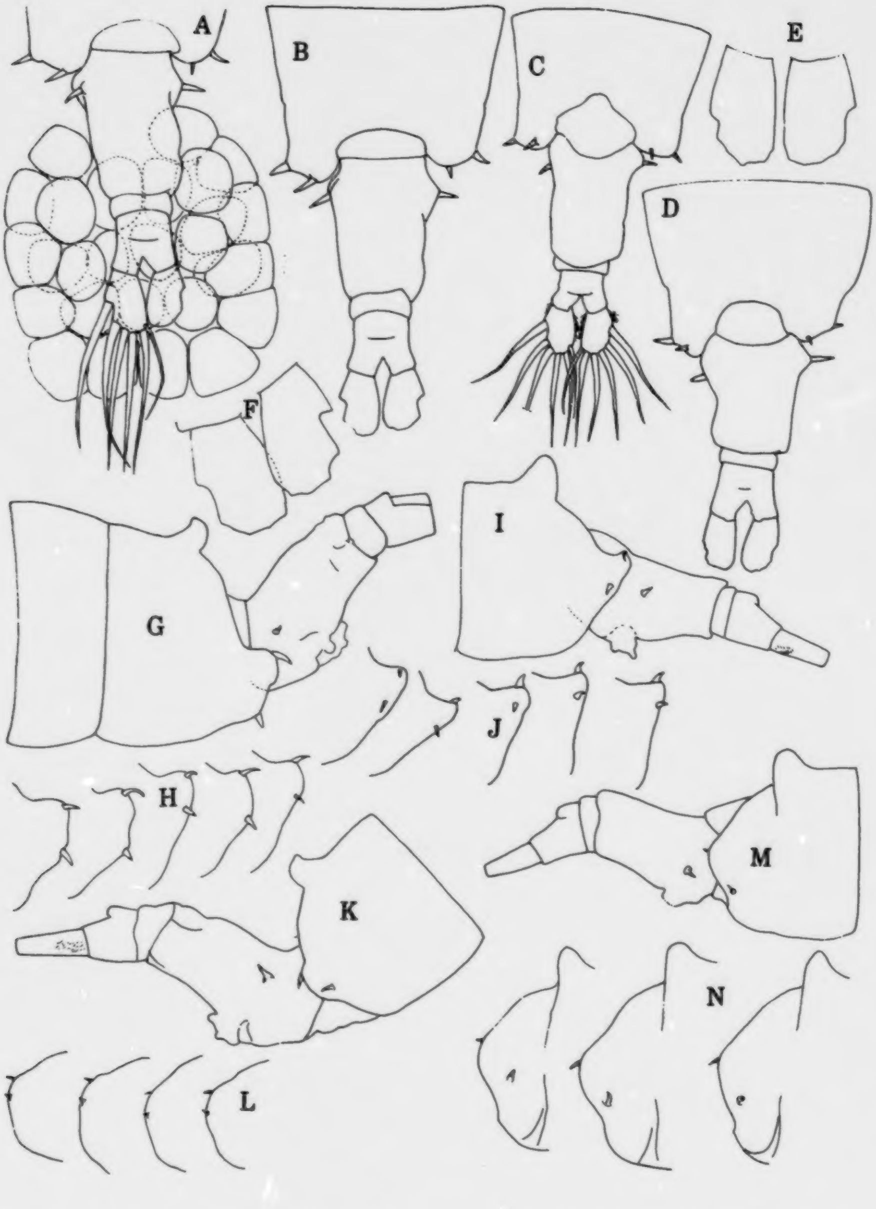

Figure 3. **A, B, F, G, H, K,** *Mastigodiaptomus nesus,* ♀, *from Pond 6, San Salvador;* **C,** *M. nesus,* ♀, *from Eleuthera;* **L,** *M. nesus,* ♀, *from Blue Hole III, San Salvador;* **D, E, I, J, M,** *M. albuquerquensis,* ♀, *from San Ignacio, Baja California Sur, Mexico;* **N,** *M. albuquerquensis,* ♀, *from near Pine, Arizona.* **A-D,** *Pediger 4∼5 and urosome, dorsal;* **E, F,** *Caudal rami dorsal;* **G, I, K, M,** *Pediger 4∼5 and urosome, lateral;* **H, J,** *Pediger 5 left wings, lateral;* **L, N,** *Pediger 5 right wings, lateral.*

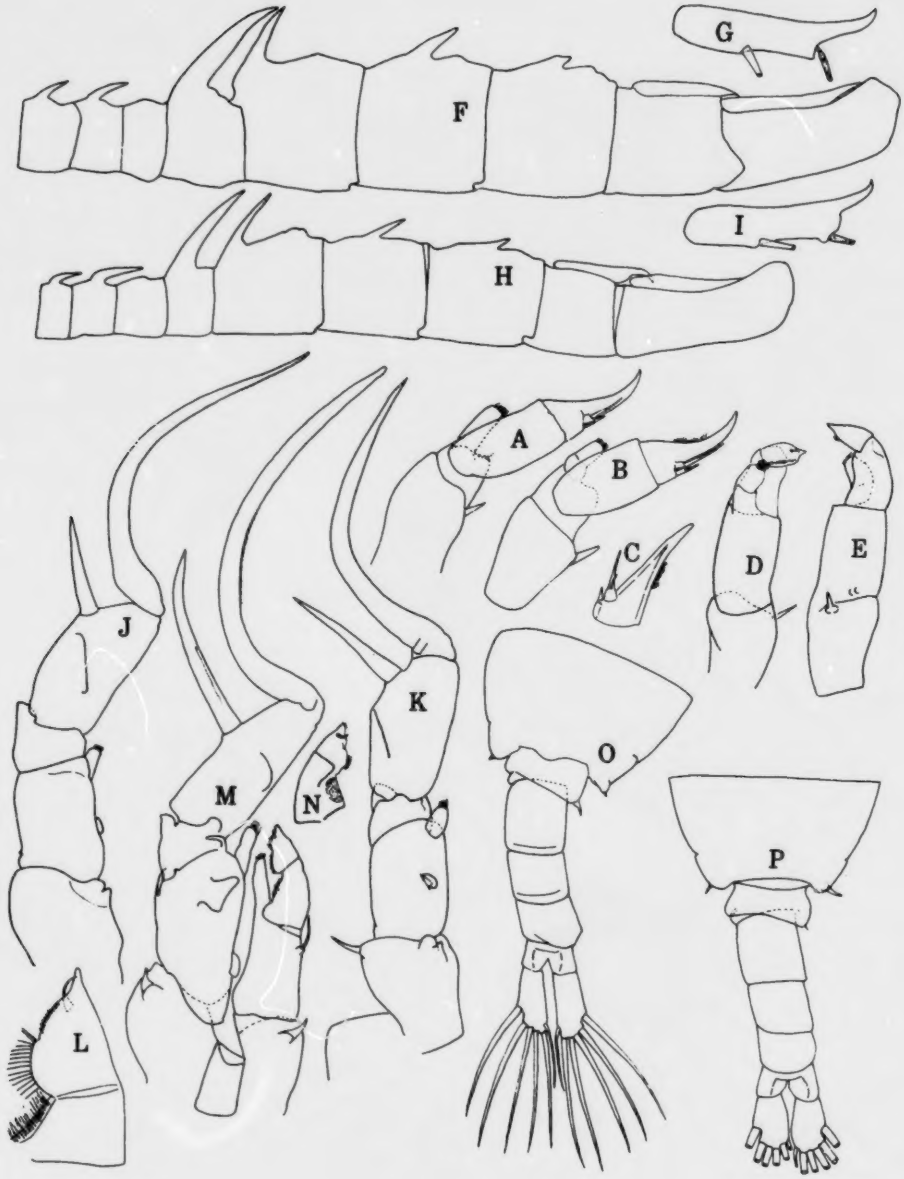

Figure 4. **A**, Mastigodiaptomus nesus, ♀, *from Grand Cayman, leg 5, lateral;* **B**, M. albuquerquensis, ♀, *from San Ignacio, leg 5, lateral;* **C**, *Distal segments of same, posterior;* **D**, **E**, M. nesus, ♀, *from Grand Cayman, anterior and posterior views of leg 5;* **F**, M. nesus, ♂, *from Pond 6, San Salvador, right antenna 1, segments 10-18;* **G**, *Same, segment 23;* **H**, M. albuquerquensis, ♂, *from San Ignacio, right antenna 1, segments 10-18;* **I**, *Same, segment 23;* **J**, **K**, M. nesus, ♂, *from Grand Cayman, right leg 5;* **M**, Mastigodiaptomus albuquerquensis, ♂, *from San Ignacio, leg 5;* **N**, *Same, apex of left leg 5, anterior;* **O**, M. albuqurquensis, ♂, *from San Ignacio, pediger 4∼5 and urosome;* **P**, M. nesus, ♂, *from Pond 6, San Salvador, pediger 4∼5 and urosome.*

Mastigodiaptomus nesus	**M. albuquerquensis**
- ♀ pediger 5 right wing, spines fairly close, ventral spine directed posteriad (Fig. 3K, L).	- ♀ pediger 5 right wing, spines well separated, ventral spine directed dorsad (Fig. 3 M, N).
- Spine on posterolateral corner of ♂ urosomite 1 weak (Fig. 4P).	- Spine on posterolateral corner of ♂ urosomite 1 well developed (Fig. 4O)
- ♀ antenna 1 reaches beyond caudal setae.	- ♀ antenna 1 reaches midlength of caudal rami.
- ♂ right antenna 1, spines on segs. 10-11 directed ca. 40° to axis (Fig. 4F)	- ♂ right antenna 1, spines on segs. 10-11 nearly parallel to axis (Fig. 4H).
- ♂ right antenna 1, spines on segs. 13-14 converging (Fig. 4F).	- ♂ right antenna 1, spines on segs. 13-14 parallel (Fig. 4H).
Right ♂ leg 5 (Fig. 4 J, K, M)	
- B1 with distomedial bilobed process	- B1 without distomedial process.
- B2 not produced proximomedially.	- B2 produced into proximomedial lobe.
- B2 without surface sclerotization.	- B2 without auricular sclerotization on posterior surface.
- Re2 with nearly straight ridge on posterior surface.	- Re2 with curved ridge on posterior surface.
- Lateral spine close to claw, straight slightly shorter than Re2.	- Lateral spine not close to claw, curved, longer than Re2.
- Claw nearly straight proximally, then bent.	- Claw evenly curved throughout.
Left ♂ leg 5 (Fig. 4L, N)	
- Distal process with smooth apex.	- Distal process with denticulate apex.

Specimens of M. nesus from Cuba have not been available, but the illustrations of M. albuquerquensis by Smith and Fernando (1978: figs. 2-4; 1980, fig. 4A-C) clearly depict M. nesus.

Origin. - Mastigodiaptomus nesus must have evolved from the only known closely similar species, M. albuquerquensis, or from a common ancestor to both species. Mastigodiaptomus albuquerquensis ranges from Utah and Colorado to Guatemala and Yucatan (Fig. 5). It is frequently found in temporary ponds in arid regions and is preadapted for the kinds of habitats occupied by M. nesus, which include ponds that dry up seasonally. The most likely origin of M. nesus is by dispersal from southern populations of either M. albuquerquensis or the ancestral continental species. Resting eggs have not been documented for M. albuquerquensis, but there is little doubt that they do occur; they are essential for survival during dry phases of temporary ponds. Resting eggs can be carried to new localities in mud on the feet of birds or on some flying insects, or by the wind. The route suggested by fig. 5 is from the Yucatan Peninsula to Cuba and The Cayman Islands, and thence to the Bahamas and Caicos.

Variation in occurrence of dorsal process of pediger 4. - In Mastigodiaptomus albuquerquensis, the dorsal process, which is present only in adult ♀♀, may be absent in some individuals of a sample, according to Wilson (1959). I am unable to verify this statement from available collections. In the following USNM samples all adult ♀♀ have a dorsal process: Arizona: Coconino Co., N. of Pine, muddy pool by road, 47 adult ♀♀, Yavapai Co., 8 mi N of Dewey, irrigation pond, 40 adult ♀♀. Mexico, Baja

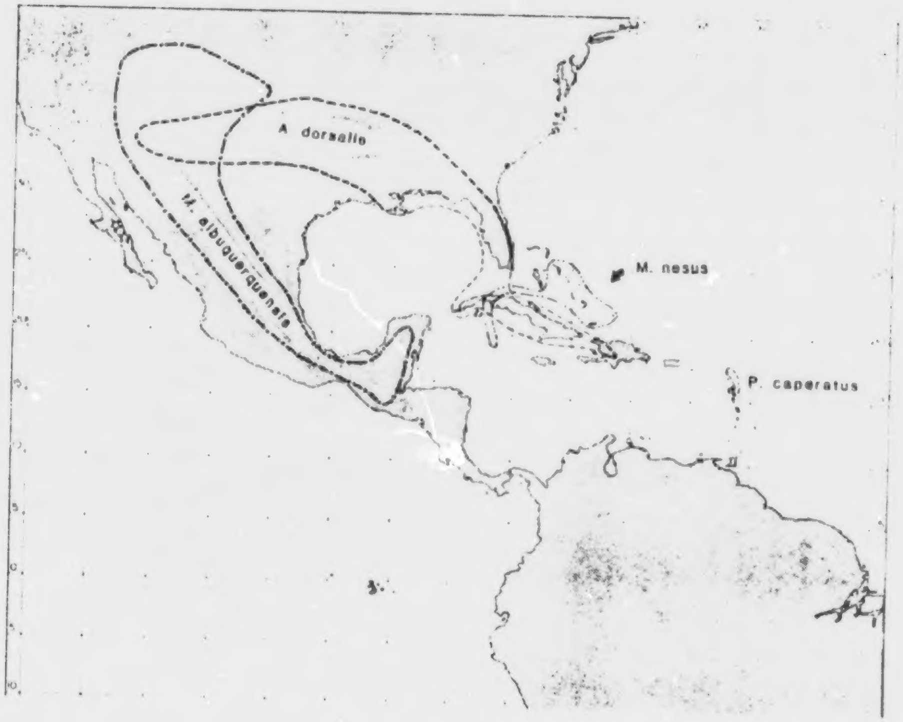
A. dorsalis
M. albuquerquensis
M. nesus
P. caperatus

Figure 5. Known distributions of West Indian freshwater calanoids and of Mastigodiaptomus albuquerquensis, the probable "parent" of M. nesus. Isolated records of the latter in Baja California are indicated by stars at San Ignacio (north) and Mulegé (south).

California: San Ignacio, permanent pool, 16 adult ♀♀. Neither Herrick (1895) nor Pearse (1904) reported a dorsal process in their specimens. Marsh (1907) thought they had overlooked it, but this seems doubtful.

The dorsal process appears to be less common in *M. nesus* than in *M. albuquerquensis*. Of the 30 University of Amsterdam samples examined only 3 contained specimens having the process. In none of these 3 samples did all adult ♀♀ have the process, but only from 40.0 to 47.7% (Fig. 1). In the small island of San Salvador, about 17 km long (Fig. 2), a dorsal process was present in 76.1% of adult ♀♀ from Barr's Pond 5, but only in 36.0% of those from nearby Pond 6. Only a few km to the south, the populations of Blue Holes III and IV completely lack the dorsal process. There must be a significant amount of isolation between the San Salvador populations. It would be instructive to know how much the frequency of the dorsal process varies with time at a particular locality. This might shed light on the question of to what extent populations of temporary and other ponds renew themselves from their own resting eggs, and whether or not there is a significant contribution of eggs from other populations.

Habitat. - About 3/4 of the University of Amsterdam samples were collected from wells. The remainder were taken from several kinds of habitat; polls, cave pools, a pothole, karst holes and clefts, and an anchialine pool ("The Hole"). Chlorinities in mg/liter ranged from 20 in a well on Eleuthera to 21326 for "The Hole". Corresponding salinities are 0.06‰ and 38.5‰. In Barr's Pond 4, 5, and 6 on San Salvador, salinities were 5, 10, and 4‰ respectively, and in Blue Holes III and IV they were 4 and 7‰. In the Blue Hole IV sample a few specimens of the coastal and estuarine calanoid *Acartia tonsa* were found. Clearly *M. nesus* can tolerate a wide range of salinities.

Arctodiaptomus dorsalis (Marsh)

In the West Indies *A. dorsalis* is found in all provinces of Cuba (Smith and Fernando, 1978) and has been reported from one locality in Haiti, Laguna Rincón, by Kiefer (1936, as *Diaptomus proximus*). In the United States it occurs in states bordering the Gulf of Mexico, and west into Oklahoma (Robertson, 1970) and Arizona (Cole, 1961). Its presence in Cuba may be attributed to dispersal from one of the Gulf states, most probably Florida, which is separated from Cuba by only a little more than 200 km.

Arctodiaptomus asymmetricus (Marsh)
Mastigodiaptomus purpureus (Marsh)

These 2 species are known only from Cuba. *Arctodiaptomus asymmetricus* has been found in Pinar del Rio, Habana, Las Villas, and Oriente provinces; *M. purpureus* has been reported only from Habana province. The origins of the 2 species are unknown. The possibilities that *M. purpureus* is derived from *M. albuquerquensis* or *M. nesus* and that *A. asymmetricus* evolved from *A. dorsalis* are worth considering.

Pectenodiaptomus caperatus (Bowman)

This species was described from Barbuda by Bowman (1979) and from Marie Galante by Dussart

(1982). Both authors consider it to be related to South American rather than to North American Diaptomidae, in contrast to the other 4 West Indian diaptomid species.

DISCUSSION

The freshwater calanoid fauna of the West Indies consists of only 5 species of Diaptomidae. Four of these, inhabiting the Bahamas and Greater Antilles, have their origins in North America. The fifth species is known from 2 small islands of the Lesser Antilles and is derived from South American ancestors. Dussart (1982) reported a total of 14 species of Copepoda from Maria Galante, all with South American affinities. He suggests that the biogeographic boundary lies between Anguilla and the Virgin Islands.

ACKNOWLEDGEMENTS

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TRAITS, PROBLEMS AND METHODS IN COPEPOD LIFE HISTORY STUDIES

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Abstract: Some methods are suggested to supplement those already used in life history studies on copepods. The areas addressed are the relationships among vital parameters, the possible effect of small population size on these parameters and geographic and temporal variation in copepod populations. The methods discussed include path analysis, least squares analysis and methods for separating genetic and non-genetic influences on copepod populations in time and space. The methods are illustrated mainly with field and laboratory data from a number of studies of the estuarine calanoid copepod Eurytemora affinis (Poppe).

In order for a species to persist individuals must survive and reproduce. The rates of survival and reproduction determine the productivity of a population. The measurements of survival and reproduction are collectively referred to as life history traits. Among the traits commonly studied in copepods are egg production, egg-to-adult viability, developmental time, sex ratio and lifespan.

The particular problems I wish to address in this paper will be discussed separately, each area being concerned with some of the above traits . These are the relationships among traits, the effects of fluctuating population sizes (inbreeding) and the effect of spatial and temporal environments on populations. The emphasis will be on methods, illustrated where appropriate with data from the copepod Eurytemora affinis (Poppe), a calanoid common in Chesapeake Bay in the eastern United States.

Some traits measurable in Eurytemora are listed in Table 1. Survival of adults, particularly in stressful environments, has been written about elsewhere (see Bradley, 1982 for references) and will not be considered here. Nor will derived measures, such as m_x, often used in life history studies, be discussed.

Table 1. *Measures of survival and reproduction in Eurytemora affinis*

Egg Production:	no. of eggs/ brood no. of broods/ lifetime
Viability:	no. of adults/ no. of eggs
Development time: (or age at first reproduction)	from egg to adult
Adult survival:	through reproductive period predicted by tolerance assays)

Egg production is observed by isolating ovigerous females under a binocular microscope and counting the eggs in the egg sac. Estimates have been checked by counting nauplii released and the accuracy is high for up to 50 eggs.

Viability is measured by counting numbers of animals in each brood at maturity, expressed as a fraction of egg count.

Sex ratio is simply the number of females over the number of adults.

Developmental time is the time from egg hatching until median maturity, an approximate measure. When the measurement is egg to egg then development time becomes age at first reproduction.

RELATIONSHIPS AMONG LIFE HISTORY TRAITS

Means and variances of four traits in three populations of Eurytemora are shown in Table 2. Commonly the first step in the study of relationships among life history traits is to measure the linear correlations and arrange them in a correlation matrix. To understand the relationships more carefully, at least two additional steps can be taken. One is to test for non-linearity. For example, in the August population higher order regression equations did not improve the fit over the linear regression of copepodids on naupliar number. Hence we conclude that there is no intermediate optimum number of nauplii for which the number of surviving copepodids is maximized. Testing for linearity of the relationship between number of females and number of adults reveals that sex ratio, 0.80 in this case, did not depend on mature brood size. The regression of female on adult number was 0.86 ± .08, and no non-linear terms were significant.

Table 2. *Means and standard deviations of numbers per brood in three different populations of Eurytemora affinis*

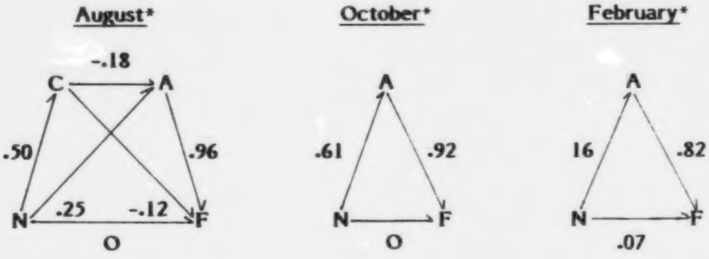
	August	**October**	**February**
Nauplii	28.8 ± 10.7*	22.0 ± 12.7	15.5 ± 4.0
Copepodids	14.6 ± 6.9	12.4 ± 8.7	--
Adults	3.2 ± 3.1	11.9 ± 8.6	5.8 ± 4.0
Sex Ratios	0.80± .06	0.43± .02	0.53± .03
Observations (brood)	76	54	48

* Standard deviations of the means (standard errors) are given by $1/\sqrt{n}$ times the standard deviations shown, where n is the number of observations used in estimating the mean.

The second step beyond the correlation matrix is to examine causes and effects among all the variables together. The analysis, known as path analysis, was first proposed by Sewall Wright in 1921. A full account appears in Wright (1968) and an elementary description in Chapter 12 of C.C. Li (1955).

In Table 3 the path diagrams for the three populations are shown. For each relationship, other than nauplii-females, the path coefficients are almost the same as the correlation coefficients; so the latter are not shown. Path coefficients are statistically similar to standard partial regression coefficients of multiple regression, but allow for complex cause and effect networks. Their benefit is in revealing relationships between cause and effect free of the effects of any other relationships in the analysis. In the case of the three populations in Table 3, the influence of naupliar number on the number of females is entirely indirect. Thus the high sex ratio (proportion of females) in August was not a result of higher mortality of male nauplii, always assuming that sex has been decided at the naupliar stage. Should these results be confirmed by other data, two factors influencing sex ratio (brood size and male mortality) would be eliminated. However, sex ratios are influenced by many environmental factors (see the review by Heinle, 1981) and the mechanism of sex determination is still unclear.

Table 3. *Path diagram showing relationships of numbers of copepods at different life stages*



Correlation NF: 0.34 0.54 0.20

Key: **N:** Nauplii, **C:** copepodids, **A:** adults, **F:** females
* Same three populations as in Table 2

FLUCTUATIONS IN POPULATIONS SIZE

Survival of small populations depends partly on the persistence of the environmental or biological constraint and partly on the resistence of the species to inbreeding, that is breeding among close relatives. Inbreeding usually affects reproductive traits more than others, hence the threat to already small populations. Systematic inbreeding is one method for testing the possible consequences of restricted population size.

For the study with Eurytemora, two rates of inbreeding were used, both operationally convenient. Ovigerous females were isolated to begin the lines. For full sib lines, females were isolated from their siblings after insemination. In some generations and in some lines more than one such female was isolated, thus splitting the original line. Double first cousin lines were maintained by matings between males and females with one set of grandparents but two sets of parents. The latter rate of inbreeding is about half the former. Control animals were sampled from stock cultures.

Data were collected each generation on egg production, egg-to-adult viability, sex ratio and development time from egg to adult. The criterion for change due to inbreeding was the regression of trait mean on generation number. However, such analysis would be misleading unless all generations were represented by the same lines. Later generations included fewer lines since many lines disappeared. The preliminary analysis suggested here estimates unbiased (least squares) means by setting up and solving equations as follows:

$$Y_{ijk} = \mu + \alpha_i B_i + \beta_j G_j + \epsilon_{ijk}$$

where Y_{ijk} is the observation, μ is the overall unbiased mean, α_i and β_j are the (least squares) effects of the ith brood or line and jth generation, B_i and G_j are binary variables (0 or 1, absent or present) and ϵ_{ijk} is the error term. The goal is to minimize the sum of the squares of the difference between the observed and predicted values of each observation, to minimize

$$\sum \epsilon^2_{ijk}$$

The method is similar to that used in Bradley (1978) to remove biases due to unequal subclass numbers in genetic variance analyses. Without the laborious details, the method consists of treating each generation and brood as a separate variable, each with two levels. For brood 1, variable B_1, would have value 1 and the others 0; similarly for variables G_j. Thus each observation has a separate equation and solving these equations simultaneously using standard multiple regression analysis yields the least squares effect of each line and generation. The unbiased generation means can then be regressed on generation number. The results are shown in Table 4. The overall conclusion is that, considering the controls, none of the traits except viability is much affected by inbreeding. This agrees with Battaglia's (1970) observations on marine and brackish water races of the copepod Tisbe furcata.

Table 4. *Changes in four traits under two rates of inbreeding in Eurytemora affinis*

Regression of (least squares) means on generation

Egg number	- .67	± .28	Full sib
(per egg sac)	- .05	± .42	Double First Cousin
	-1.61	± .86	Control
Viability	-2.3	± .48	Full sib
(% egg to adult)	-5.3	± 1.0	Double First Cousin
	- .01	± .02	Control
Sex Ratio	+2.9	± 1.4	Full sib
(°/TOT %)	- .06	± 1.4	Double First Cousin
	0.03	± .03	Control
Developmental time	- .22	± .41	Full sib
(egg to adult)	-1.23	± .64	Control

DIFFERENTIATION AMONG POPULATIONS

Eurytemora and other copepods are subject to a wide range of geographic and seasonal conditions. The consequent differentiation in reproductive traits may be physiological or genetic. Genetic differences are almost always small compared to non-genetic differences, especially in traits important to survival where the conventional wisdom is that most of the genetic variance has disappeared. Such may not always be the case (see McLaren, 1976 and the recent symposium on the evolution and genetics of life histories (Dingle and Hegman, 1982)).

The general method for characterizing spatial or temporal variation is to observe the traits of interest at two or three levels - in the wild-caught (parental) animals from different places or times, in the F_1 generation and possibly in the F_2 generation. Variation among **parental means** is the result of physiological (short-term) and genetic (long-term) effects of the environments. Variation among F_1 **progeny** raised under uniform laboratory conditions is due to genetic and maternal influences and variation among F_2 **progeny** to genetic effects (and to grand-maternal effects which are unlikely). From these data, observed geographic or seasonal differences in populations can be identified as physiological or genetic or both.

The method was used by Wyngaard (1983) to demonstrate genetic differences in maturation time, body size and clutch size between populations of the freshwater copepod *Mesocyclops edax* in Michigan and Florida lakes. I have used the method to test for genetic divergence among three constant and two cycling temperature regimes in the laboratory (Bradley, 1982). Egg production, viability and sex ratio of *Eurytemora affinis* differed significantly among regimes at the parental level, but not at the progeny level, when the progeny were all grown at 15°C. This indicated that the populations diverged, but not genetically.

Table 5. *Egg counts from E. affinis at three stations at Crane Power Plant on four dates in 1982*

	Intake	Discharge
April 1982	22.8	15.0
Temp.	13.4°C	16.8°C
No of obs.	22	18
May 1982	34.4	21.2
Temp.	20.9°C	25.9°C
No of obs.	13	5
June 1982	39.4	49.6
Temp.	26.8°C	30.1°C
No of obs.	13	9
December 1982	43.4	58.2
Temp.	8.5°C	11.4°C
No of obs.	25	21

	Significance: Intake v. discharge
April	**
May	**
June	n.s.
December	*

* = p .05
** = p .01
n.s.= not significant

Seasonal differences in the wild were also tested by comparing trait means of parents and progeny. In this case, means were regressed on ambient temperature. I have shown that trends in temperature tolerance of *Eurytemora*, the trait I have been primarily concerned with over the years, were mainly nongenetic. The regression of parental means on ambient temperature was significant, but that of progeny means was not (Bradley, 1982). I have also shown that the regression of egg production on temperature was -1.17 ± .44, based on 32 observations over 2 years in a range of temperatures from 7.5 to 24°C. If we had also measured progeny egg production we would have established whether this significant trend was partly genetic.

Data on spatial variation in egg production are shown in Table 5. Again progeny egg counts were not taken, but, in an earlier more extensive study, progeny egg counts were obtained. Unfortunately, because of the original purposes of the studies, parental counts were not obtained in one case and progeny counts were not available from the other. Nevertheless the inference can be drawn from Tables 5 and 6 together that spatial variance in egg production is mostly environmental. Note that egg production and temperature are not linearly related, suggesting, not surprisingly, an optimum temperature for egg production.

Table 6. *Egg production and sex ratio in progeny of E. affinis adults collected in April 1981 at a power plant discharge (Crane) and at a reference area (Bear Creek).*

	Egg Production	
Crane (21.8°C)	21.04	(33 families, 197 females)
Bear Creek (18.6°C)	24.15	(41 families, 288 females)

Analysis of variance (log transformed data)

	df	M.S.
Sites	1	0.437
Families/site	73	0.180**
Within families	412	0.048

** p=.01

Proportion of genetic and maternal variance in egg production

= 0.66 + 0.16

	Sex ratio (females/total)	
Crane	0.64	(33 families)
Bear Creek	0.69	(41 families)

No significant differences between sites, no variance estimates possible within families. Variance among families was 0.314.

The data in Table 6 also suggest genetic variation within the sites. There is variation among families in egg production that seems higher than would be due to maternal effect alone and sex ratio also appears to vary genetically since the distribution is wider than that expected from random binomial proportions, 0.314 compared to 0.037. Thus the absence of genetic variance among sites in egg production or sex ratio is probably not because of its absence within sites.

This paper does not pretend to be a review of methods used in copepod life history studies, much less a comprehensive review, but rather is intended to suggest some additional experimental and analytical methods which might normally be overlooked.

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FEEDING AND FOOD COMSUMPTION BY MESOCYCLOPS EDAX

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Abstract: Later copepodite stages of the cylopoid copepod Mesocyclops edax feed on the same prey species as do the adult animals, but small species of rotifers are an even more important component of their diet than of the diet of adults. Of the cladocerans preyed upon by the adults, only Bosmina longirostris was a significant component of the diet of the later copepodite stages. The younger copepodite stages preyed only on small rotifers, with a very small portion of naupliar larvae in their diet.

INTRODUCTION

Species of the genus Mesocyclops are active invertebrate predators: adults and later developmental stages feed raptorially on other zooplankters. Various aspects of their feeding were studied in both field and laboratory conditions (e.g. Brandl and Fernando, 1975, 1979; Gophen, 1977; Karabin, 1978; Kerfoot, 1978; Williamson, 1980; Jamieson, 1980). However, the data concerning Mesocyclops edax were obtained either in laboratory experiments with adult animals (Brandl and Fernando, 1975; Williamson, 1980, 1981, 1983) or in field measurements dealing with the whole predator population together (Brandl and Fernando, 1978, 1979). The aim of our present contribution was therefore to estimate predation rate of the predatory larval stages of Mesocyclops edax and to compare it with that of adult animals.

MATERIAL AND METHODS

From August through early October, 1982, we made four series of experiments in two shallow reservoirs inhabited by populations of Mesocyclops edax: Columbia Reservoir and Laurel Creek Reservoir, both located near Waterloo, Southern Ontario, within easy access to the laboratory microscopic control of the field procedure.

Basically, we used the same method as in our previous field experiments (Brandl and Fernando, 1978). Only the separation of size fractions was more detailed. Mixed samples of zooplankton were collected from all layers from the surface to the bottom (depth less than 5 m) using a van Dorn sampler, and concentrated by a 0.04 mm plankton net. A set of sieves differing each from the next by about 0.02 mm allowed us to separate relatively narrow size fractions of animals. We tried to obtain size fractions which would contain the following categories:

1) adults of Mesocyclops edax and females of the V-th copepodite stage, hereafter called "adult animals".

2) the III-rd and IV-th copepodite stage, i.e. larger copepodite larvae.

3) the first two copepodite stages (with some - less than 10% - of the III-rd stage), i.e. smaller copepodite larvae.

Usually the sieves with mesh sizes of 0.31 and 0.21 mm separated these three categories of the *Mesocyclops* populations in the reservoirs studied. The individual size fractions contained between 4 and 9% of *Mesocyclops* specimens of neighbouring fractions mostly of the larger ones.

Desired size fractions of zooplankton were separated by careful pouring through appropriate sieves. Then the zooplankton was reconstituted with elimination of one size fraction in the control set of replicates. This size fraction was added only to the experimental series and the differences between this and the control series after 24 hours was attributed to the predation in this size fraction. The prey animals contained in this size fraction eliminated from the control set and available to predators in the experimental set were taken into account, as were their developmental stages born during the experiment. A 120 ml kitchen ladle (brimfull) was used to obtain identical replicates, with at least five doses taken from well-mixed material of known concentration into each replicate. The replicates were then rediluted with filtered lake water to the original zooplankton density in 5-litre bottles. Each experimental or control series consisted of two to five replicates for each combination of predator fractions.

RESULTS

Zooplankton of both Columbia and Laurel Creek Reservoirs in late summer and early autumn of 1982 consisted of about 20 abundant rotifer and crustacean species mostly of small size, with the total number of all specimens ranging from three to five thousand per litre. Density of all copepodite and adult stages of *Mesocyclops edax* in experiments was between 60 and $90.l^{-1}$; density of prey species was highest for the rotifers *Keratella cochlearis* ($420\text{-}199.l^{-1}$), *Polyarthra euryptera* (up to $1100.l^{-1}$) and the cladoceran *Bosmina longirostris* (510 to $1300.l^{-1}$).

Significant predation by *Mesocyclops* was for 10 species of the prey present in the reservoirs. In decreasing order of their participation in the predation of the whole *Mesocyclops* population, they were: *Filinia longiseta, Polyarthra euryptera, Bosmina longirostris, Keratella cochlearis, Pompholyx sulcata* (all these five species with average daily ration higher than 1 prey specimen per 1 predator), *Brachionus angularis,* naupliar larvae of copepods (*Diaptomus oregonensis, Tropocyclops prasinus, Mesocyclops edax*) - these two prey items were consumed in average between 0.2 and 0.5 prey specimen per predator per day. The last three species, *Asplanchna priodonta, Daphnia retrocurva,* and *Ceriodaphnia quadrangula,* contributed to the daily ration of the predator by less than 0.2 of prey per predator.

All these ten species were eaten by the largest, the "adult" size category of *Mesocyclops,* with the only difference that the cladocerans *Bosmina longirostris* and *Daphnia retrocurva* occupied a more important position in the prey list (see Fig. 1). Also the food of the middle category, i.e. the "larger" predatory larval stages, consisted of all these ten species, with a more important position of rotifers: *Bosmina longirostris* being only the fifth one. When daily rations of this size category are compared with those of the "adult" category (Table 1), they are mostly 60-70% of the latter for rotifers and naupliar larvae, and much less for cladocerans. For the smallest size category of the predator, i.e. the "smaller" copepodite stages, both cladocerans and the rotifer *Asplanchna priodonta* are missing from the list of prey species and the daily rations are much smaller even for rotifers, with some changes in the

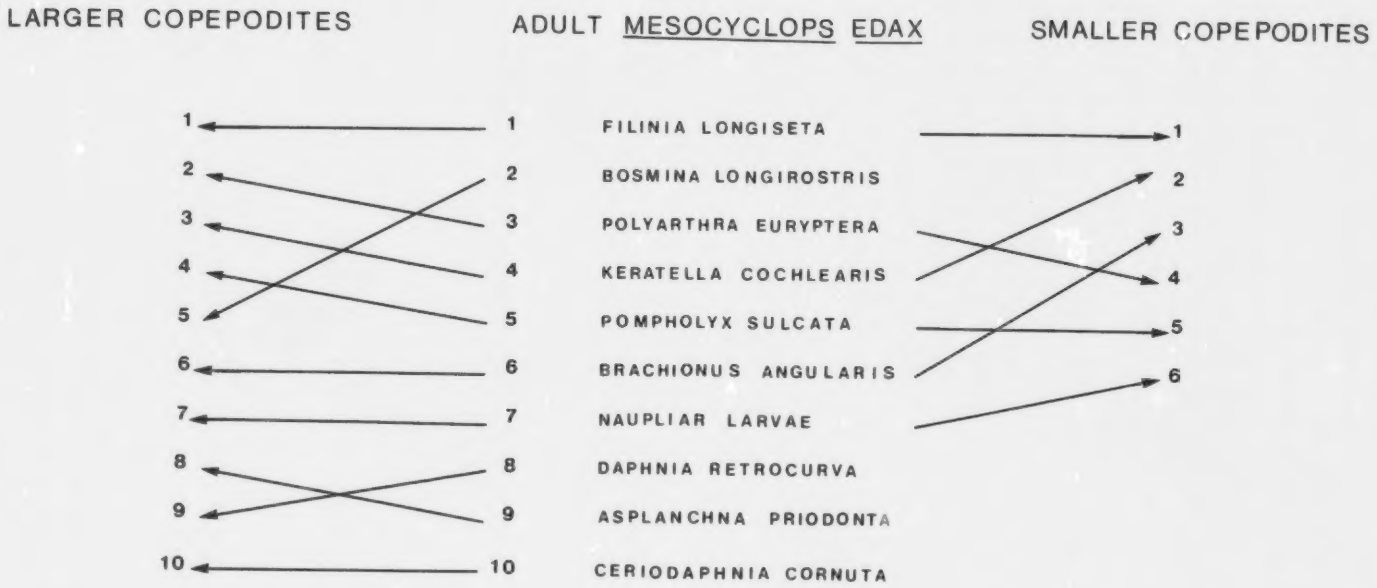
LARGER COPEPODITES
ADULT MESOCYCLOPS EDAX
SMALLER COPEPODITES
1 FILINIA LONGISETA
2 BOSMINA LONGIROSTRIS
3 POLYARTHRA EURYPTERA
4 KERATELLA COCHLEARIS
5 POMPHOLYX SULCATA
6 BRACHIONUS ANGULARIS
7 NAUPLIAR LARVAE
8 DAPHNIA RETROCURVA
9 ASPLANCHNA PRIODONTA
10 CERIODAPHNIA CORNUTA
1
2
3
4
5
6
7
8
9
10
1
2
3
4
5
6

Figure 1. *Prey species of the adult (center), the larger copepodite stages (left), and the smaller copepodite stages (right) of Mesocyclops edax arranged in the order of decreasing magnitude of the daily ration.*

order in which these rotifer species are preyed upon by the small copepodite larvae.

Table 1. *Daily food rations of the smaller and the larger copepodite larval stages of Mesocyclops edax in % of the daily rations of adult animals.*

Prey species	**Smaller copepodite stages**	**Larger copepodite stages**
Filinia longiseta	18	52
Polyarthra euryptera	5	69
Keratella cochlearis	3 - 49	60 - 70
Brachionus angularis	8 - 30	49 - 73
Pompholyx sulcata	6	60
Asplanchna priodonta	0	53
naupliar larvae	5 - 13	69 - 76
Daphnia retrocurva	0	20
Ceriodaphnia quadrangula	0	50
Bosmina longirostris	0	23 - 49

DISCUSSION

Our data from the field experiments revealed that the animal prey of the predatory developmental stages of Mesocyclops edax consists of the prey species which are also preyed upon by the adult copepods. Younger copepodite stages preyed on small rotifers in some extent but much less than adults did. Later copepodite stages were significant predators of small rotifers, naupliar larvae and Bosmina longirostris. Low values of daily rations of the younger copepodite stages (less than 0.5 prey specimen per predator for any prey species) suggest that there might be another - i.e. algal - source of food for these developmental stages. Although we earlier (Brandl and Fernando, 1979) found that M. edax did not consume Ceratium, other large algae may be readily consumed (e.g. Peridinium: Williamson and Magnien, 1982) even by adult M. edax. Early copepodite stages of the related species Mesocyclops leuckarti (= M. spp.) were reported to feed exclusively on algae (Gophen, 1977) although Jamieson (1980) found copepodite stage III of the same species to be predatory. This author has also shown the increase of daily rations from one copepodite stage to the next, as well as an expanding spectrum of prey species (or types) from the III-rd copepodite stage to adults. A narrower prey spectrum of younger copepodite stages and thus predation on cladocerans only by later and adult stages might also explain a much higher impact of Mesocyclops predation on rotifers than on cladocerans that we have found earlier (Brandl and Fernando, 1979). Thus, besides the spatial arrangement of predator and prey populations (Williamson and Magnien, 1982) also temporal changes of the composition of the predator's population may play a decisive role in determination of the impact of predation by cyclopoid copepods on zooplankton.

ACKNOWLEDGEMENTS

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PLANKTOBENTHIC COPEPODS FROM THE SOUTHERN BRAZILIAN CONTINENTAL SHELF

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Abstract: Copepods from 21 samples collected with a 0.670 mm meshed bottom net trawled over the southern Brazilian continental shelf are qualitatively and quantitatively analysed. Based on distributional and morphological characters, the planktobenthic copepod fauna is tentatively characterized in its truly planktonic component and its bottom-associated component, both from shallower (15-50 m depth) and deeper (72-150 m depth) bottom waters. *Calanoides carinatus* is the most representative planktonic species in both habitats, followed by *Temora stylifera*, *Eucalanus pileatus* and *Calanopia americana*: the bottom-associated component is only found in the deeper waters and represented, in decreasing order of importance by *Brachycalanus bjornbergae*, *Xanthocalanus marlyae*, *Bradyidius plinioi*, *Paracomantenna magalyae*, *Parapseudocyclops giselae*, *Scolecithricella pseudoculata*, unidentified Cyclopidae and a misophrioid.

INTRODUCTION

Qualitative and quantitative studies on shallow-water planktobenthic copepod fauna (vide references in Fosshagen 1978, Wishner 1980, and Youngbluth 1982) are relatively few, as are those on deepwater fauna (references in Wishner 1980). The collecting methods employed until now, although efficient for a particular type of substrate or group of copepods, have been the main obstacle to a comprehensive study of the structure and functioning of this community.

Epibenthic, planktobenthic, hyperbenthic (vide Campaner 1978), demersal (vide Youngbluth 1982), natant (Bossanyi 1957), and benthopelagic (Wishner 1980) have been some of the terms used to refer to such free-swimming copepods living close or in some way related to the bottom. The planktobenthos should be considered an ecotone between the benthos and the plankton, without clear delimination in space (Boysen 1975).

During 1970, the R/V 'Prof.W.Benard' of the University of Sao Paulo performed a cruise in which planktobenthic samples were collected over the southern Brazilian shelf and slope with a special trawl built in the Instituto Oceanográfico, University of São Paulo, under the supervision of Dr. Plínio Soares Moreira, who named it 'Mini Biological Trawl' (MBT).

The qualitative and quantitative copepod composition of 21 samples from MBT collection taken over the shelf is analysed here. The characterization of the planktobenthic copepod fauna for the studied area is tentatively established.

STATION DATA, MATERIALS AND METHODS

Figure 1 shows the positions of the stations. Date, collecting depth, starting time (hr) of the collection on the bottom, and bottom water temperature and salinity, when available, for each station are respectively the following:

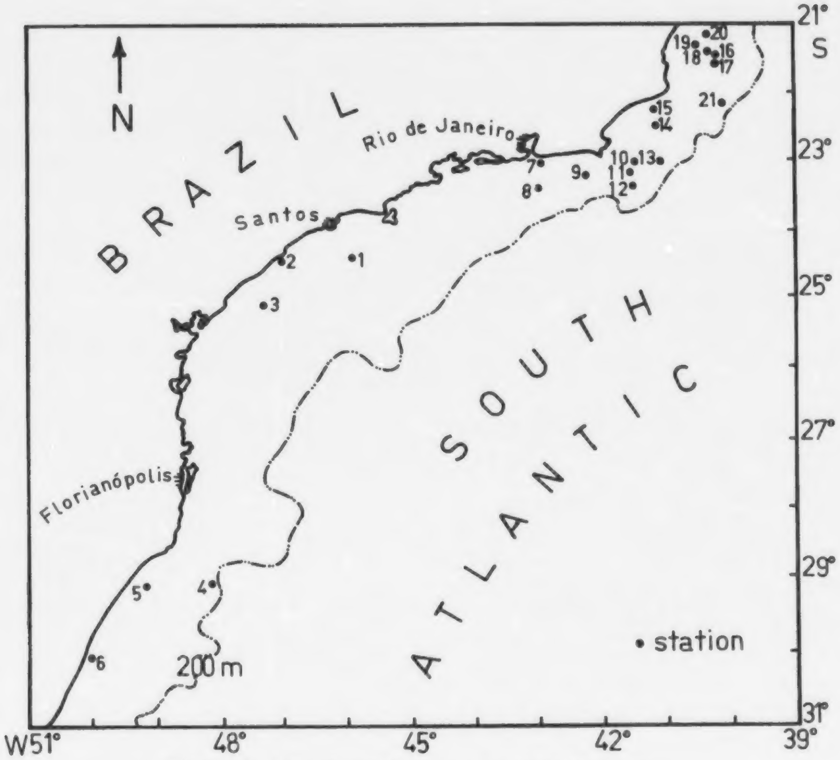
N
BRAZIL
Rio de Janeiro
Santos
Florianópolis
SOUTH ATLANTIC
• station
200 m
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
21°
S
23°
25°
27°
29°
31°
W51°
48°
45°
42°
39°

Figure 1. *Station positions in the sampling area.*

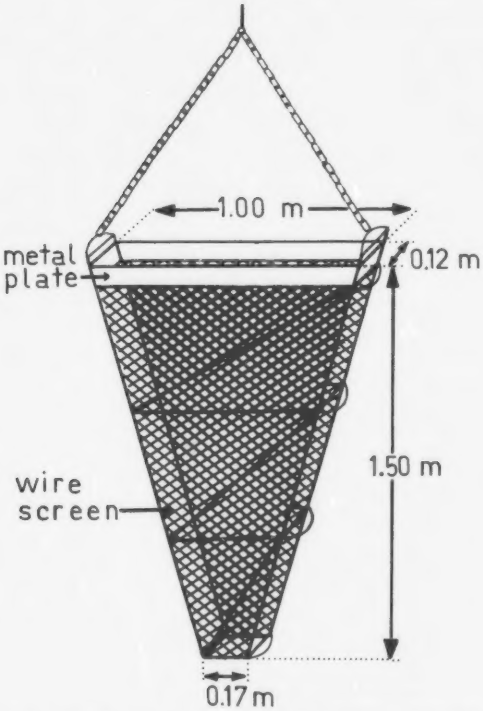
1.00 m
metal plate
0.12 m
1.50 m
wire screen
0.17 m

Figure 2. *Sketch of the metal frame of the 'Mini Biological Trawl' (MBT), in upright position.*

Table I. *Occurence and abundance of copepod species in the planktobenthic samples. Numbers of individuals of each species at every station of Fig. 1.*

SPECIES/ STATION	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
CALANOIDA																					
Family Calanidae																					
Calanoides carinatus (Kroyer 1849)	4						253	59	1	60	276	16	323	4	19	2	60	70	3	2	1
Calanus minor (Claus 1863)				1									1								
Neocalanus gracilis (Dana 1849)				2																	
Undinula vulgaris (Dana 1849)	4																	1			
Calanidae		1											2		1						1
Family Eucalanidae																					
Eucalanus crassus Giesbr. 1888													1								
E. pileatus Giesbr. 1888	1		18		1	20	48	3		15	3	3	44	1	1	10	48	11	18	4	
Family Paracalanidae																					
Acrocalanus longicornis Giesbr. 1888			1																		
Paracalanus aculeatus Giesbr. 1888			4										4				16	2			
P. campaneri Bjornberg 1980		17															10				
P. indicus Wolfenden 1905		3															31				
Paracalanus sp.		1					1										17	1			
Family Pseudocalanidae																					
Clausocalanus arcuicornis (Dana 1849)							5				1		3								
C. furcatus (Brady 1883)	3		3									6	8				3	2			
C. ingens Frost & Fleminger 1968							6						5								
C. parapergens Frost & Fleminger 1968											1										
Clausocalanus sp		1									11		1								
Ctenocalanus vanus s. l. Giesbr. 1888							1			1											
Family Aetideidae																					
Bradyidius plinioi Campaner 1978				1				9			14	1									
Paracomantenna magalyae Campaner 1978								8			10	1									
Family Euchaetidae																					
Euchaeta marina (Prestandrea 1833)				3		2		1													
Family Phaennidae																					
Brachycalanus bjornbergae Campaner 1978	2									7	43	3	6								
Xanthocalanus marlyae Campaner 1978								1			40	2	3								
Family Scolecithricidae																					
Scolecithricella pseudoculata Camp. 1979											1										
Scolecithrix danae (Lubbock 1856)				1																	
Scolecithricidae											2										
Family Temoridae																					
Temora stylifera (Dana 1849)	2		10	1		10	57	1		36	4	3	26		1	4	12	26	7		
Family Metridinidae																					
Pleuromamma abdominalis (Lubbock 1856)								1			6	4	16								
P. gracilis (Claus 1863)								1					4								
P. piseki Farran 1929													17								
P. xiphias (Giesbr. 1889)													1								
Pleuromamma sp													2								

Table 1 (continued)

SPECIES/ STATION	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Family Centropagidae																					
Centropages velificatus (de Oliviera 1946)			3			6	7			1		2	2			3	46	3	5	4	
Family Pseudodiaptomidae																					
Pseudodiaptomus acutus (F. Dahl 1894)	1																				
Family Lucicutiidae																					
Lucicutia flavicornis (Claus 1863)													1								
Lucicutia sp.								1													
Family Heterorhabdidae																					
Heterorhabdus papilliger (Claus 1863)				2				5			1	1						1			
H. spinifrons (Claus 1863)													6								
Family Arietellidae																					
Parapseudocyclops giselae Campaner 1977											2										
Family Candaciidae																					
Candacia bipinnata (Giesbr. 1889)						3	7	3			3		2	1							
C. curta (Dana 1849)			2	2			12						5					1			
C. pachydactyla (Dana 1849)				1																	
Candacia sp.													12								1
Family Pontellidae																					
Calanopia americana F. Dahl 1894		3	6				12	4		1	2	2	3		1	3	26	8	6	1	
Labidocera acutifrons (Dana 1849)																	1				
L. fluviatilis F. Dahl 1894			2		1	1				8											
Pontellopsis brevis (Giesbr. 1889)			8		2		1			3						2					
Family Acartiidae																					
Acartia lilljeborgi Giesbr. 1889			1																		
CYCLOPOIDA																					
Family Oithonidae																					
Oithonia fallax Farran 1913												1									
Family Cyclopidae																1					
POECILOSTOMATOIDA																					
Family Oncaeidae																					
Oncaea venusta Philippi 1843													1								
Family Sapphirinidae																					
Copilia mirabilis Dana 1849			2																		
Family Corycaeidae																					
Corycaeus amazonicus F. Dahl 1849							1				2		3				4				
Family Clausidiidae																			1		
Family Lichomolgidae				1						2	2										
SIPHONOSTOMATOIDA																					
Family Dyspontiidae													1								2
MISOPHRIOIDA																					
unidentified misophrioids												1									
HARPACTICOIDA																					
Longipedia coronata Claus 1863						1	1														
unidentified benthic harpacticoids	1																16				

STATION	DATE	DEPTH (m)	TIME (hr)	TEMP. (^{o}C)	SALINITY (o/oo)
1	16. June 1970	72	15:23		
2	17. June 1970	35	11:51		
3	18. June 1970	35	03:55	19.70	35.85
4	24. June 1970	135	23:27		
5	25. June 1970	27	18:54		
6	26. June 1970	25	10:56		
7	02. Sept. 1970	43	06:42	5.55	35.68
8	02. Sept. 1970	115	13:45	4.56	35.47
9	03. Sept. 1970	120	09:22	3.14	35.32
10	03. Sept. 1970	75	18:43	1.62	35.05
11	03. Sept. 1970	100	21:30	1.67	34.92
12	04. Sept. 1970	150	02:18	5.13	35.57
13	04. Sept. 1970	97	19:41	9.44	36.28
14	04. Sept. 1970	50	22:44	3.01	35.28
15	05. Sept. 1970	30	04:31	4.40	35.43
16	05. Sept. 1970	15	13:03		
17	05. Sept. 1970	35-37	17:18		
18	06. Sept. 1970	25	06:37		
19	06. Sept. 1970	17	09:35		
20	06. Sept. 1970	19	12:23		
21	06. Sept. 1970	50	20:37	15.52	35.61

The MBT is a modified 'Small biology trawl' (Menzies 1962: 85, fig.1). The net bag is made of nylon cloth 0.670 mm mesh, and attached to the inside of a trapezoidal metallic frame (Fig.2). Due to its small weight (29 kg), the MBT digs only superficially into the sediment. Thanks to this, the trawl is especially efficient in collecting small animals present on and/or just over the surface of the sediment. Despite the permanently open net mouth, the narrow trawl opening prevents the sediment from being washed out during the ascent of the net, and contamination by pelagic forms from the water column is very low.

Copepods were sorted from the sediment gathered by the collection net when trawled during about 15 minutes along the bottom surface.

RESULTS AND DISCUSSION

Table I shows the occurence and abundance of the copepod species identified. Shallower stations (from 15 to 50 m depth) yielded common species usually caught in vertical or oblique towings of standard nets, whereas less common species only appeared in the deeper stations (from 72 to 150 m depth).

Among the six stations with greater specimen numbers (Fig.3), three are shallower (St. 7, 17 and 18), and the remaining are deeper ones. In all of them, the collectings started either in the evening or at dawn.

Calanoides carinatus was the most frequent and abundant species, followed by *Temora stylifera* and *Eucalanus pileatus*. These three species were also the most important constituents in oblique towing samples taken from 5 m above the bottom to the surface, in the area corresponding to the stations 10, 11 and 13 (Campaner, unpublished data). *Calanoides carinatus* is restricted to the South Atlantic Central Water over the shelf, while the other two species also occur in the shallower Shelf Water and

Tropical Water masses, concentrating near the bottom during and near the surface at night. The co-occurence of *Calanopia americana*, *Centropages velificatus*, *Labidocera fluviatilis* and *Paracalanus* spp. are not surprising, as the first has been usually found over the bottom and even penetrating into the sediment surface (Bradford 1969), and the other three seem to seek the shallow near-bottom waters for food, protection and reproduction. Most of the females of *C. velificatus* and *L. fluviatilis* bore attached spermatophores, which might indicate that some of their eggs are laid on the sediment, as reported for some other species of these two genera (Grice and Marcus 1981).

Among the less common species identified, *Xanthocalanus marlyae* has been the sole species collected in the oblique towing samples already mentioned. *Scolecithricella pseudoculata* and *Bradyidius plinioi* may be similarly collected, whereas *Brachycalanus bjornbergae*, *Paracomantenna magalyae* and *Parapseudocyclops giselae* seem to live closely associated with the sea floor. According to Marcotte's (1983: 48) picture of the representative copepod species, the first three mentioned species approach the natant type and the three remaining species the epibenthic type.

These last three species have all the characters considered as an adaptation to the bottom-living existence, such as a plump body, a short 1st antenna, strong outer spines on the swimming leg exopods (Bowman and González 1961), a setose 1st antenna (Matthews 1964), a reduction or even the absence of the mandibular endopod, and a strong maxilliped (Fosshagen 1970). In addition, Matthews (1964) recorded adaptations related to the reproduction for some other planktobenthic species, such as a reduced egg production, reduced and simplified naupliar stages, and a less fortuitous egg attachment to the substrate.

In conclusion, it may be said that these copepods usually present similarities of the body shape, the 1st antenna and swimming legs; the structure of the mouthparts, particularly involved in feeding is however diversified (Campaner 1977). The swimming and other movements described by Bowman and González (1961) and Fosshagen (1968, 1978) for some species probably constitute a general pattern for the truly planktobenthic species, and confirm the apparent morphological similarities of the appendages involved in these movements.

Concerning the feeding habits, *Bradyidius plinioi*, *Xanthocalanus marlyae*, *Brachycalanus bjornbergae* and *Paracomantenna magalyae* could be scavengers, as suggested by Matthews (1964) for some Norwegian planktobenthic aetideids and phaennids. Thus, these and other planktobenthic and even planktonic species appear to seek food in the flocculant zone at the surface of the sediment. Conspicious differences in the mouthparts, especially among genera, suggest different feeding habits and, by extension, a large niche partitioning.

According to Wishner (1980), the deep-sea planktobenthic community can be divived into a truly planktonic component and a bottom-associated component, but some copepods belonging to this last assemblage appear to move freely from the bottom to at least 10 m above it. These features can be recognized here too.

Thus, based on my comments on Table I and Figure 3, the planktobenthic copepod community over the southern Brazilian shelf can be characterized as follows:

(i) Shallower water community (15-50 m depth). - Apart from benthic harpacticoids and *Calanopia americana*, only planktonic species were recorded. From these, *Calanoides carinatus*, *Temora stylifera*, *Eucalanus pileatus*, *Centropages velificatus*, *Paracalanus* spp. and *Clausocalanus* spp. were the most representative species.

(ii) Deeper water community (72-150 m depth). - The planktonic component dominated by *Calanoides carinatus*, followed by *Temora stylifera* and *Eucalanus pileatus*. The bottom-associated

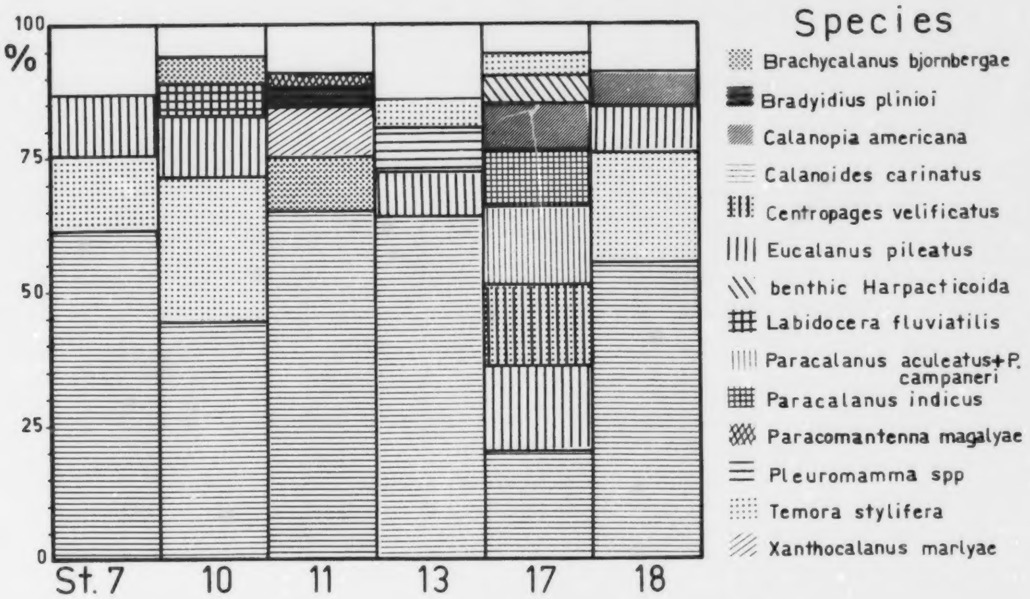

Figure 3. *Relative percentage of species composition in the most abundant six stations.*

component represented, in decreasing order of importance by Brachycalanus bjornbergae, Xanthocalanus marlyae, Bradyidius plinioi, Paracomantenna magalyae and, as rare species, Parapseudocyclops giselae, Scolecithricella pseudoculata, unidentified Cyclopoidae and a misophrioid. From these planktobenthic species, X. marlyae seems to move between the bottom and at least 5 meters above it, the same could happen with B. plinioi and S. pseudoculata; the remaining species are in closer association with the bottom.

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AN ECOLOGICAL STUDY OF THE PLANKTONIC COPEPODA OF THE SOUTH CHINA SEA

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Abstract: This paper is based upon the study on the material collected from some large estuaries, the continental shelf and slope, and the deep basin of the South China Sea, comprising Xisha, Zhongsha and northern Nansha Islands areas from 1976 to 1982.

The general trend of the quantitative horizontal distribution of planktonic copepods in this region is a decrease in abundance with the increase of distance from shore. But in some months, the abundance of planktonic copepods in the shelf water is greater than that in the nearshore area.

The quantitative vertical distribution of the planktonic copepods is inhomogeneous. The greatest abundance is located in the 0-100 m layer. In the layers lower than 100 m there is a marked decrease in abundance with the increase of depths.

In the estuarine and nearshore areas, the quantity of planktonic copepods shows an obvious seasonal variation. In general, the abundance of these animals in different seasons is more or less stable on the continental slope and in the deep sea basin.

A number of planktonic copepod species exhibit diurnal migration. Hence, the greatest abundance occurs in the 50-100 m layer in daytime and in the upper 50 m at night.

INTRODUCTION

Copepods are the most abundant group of planktonic crustaceans, both in biomass and in number of species in the South China Sea. Nearly 400 species have been recorded and, as a group, they usually constitute 45-85% by volume of any plankton sample collected from the area. The ecology of copepods is related to the secondary productivity and the spatial and temporal structure of the water column and hence highly related to the fishery. Studies on copepods of this area are scarce (Fleminger, 1963; Wickstead, 1961). The purpose of this paper is to describe the quantitative distribution, seasonal variation in abundance, and diurnal vertical migration of copepods, and the use of some copepod species as biological indicators in the South China Sea.

MATERIAL AND METHODS

This report is based on plankton samples collected from the waters adjacent to the following areas in the South China Sea (Fig. 1):

1. Xisha and Zhongsha Islands (Paracel Islands and Macclesfield Banks) from 1974 to 1979.
2. Dongsha Islands (Pratas Islands), including the southern part of Taiwan Strait and the northeastern Philippines, from 1979 to 1983.
3. Nansha Islands (reef islands around Investigator Shoal), from June to July 1984.

Samples were collected from vertical tows using nets with opening and closing mechanisms. Two

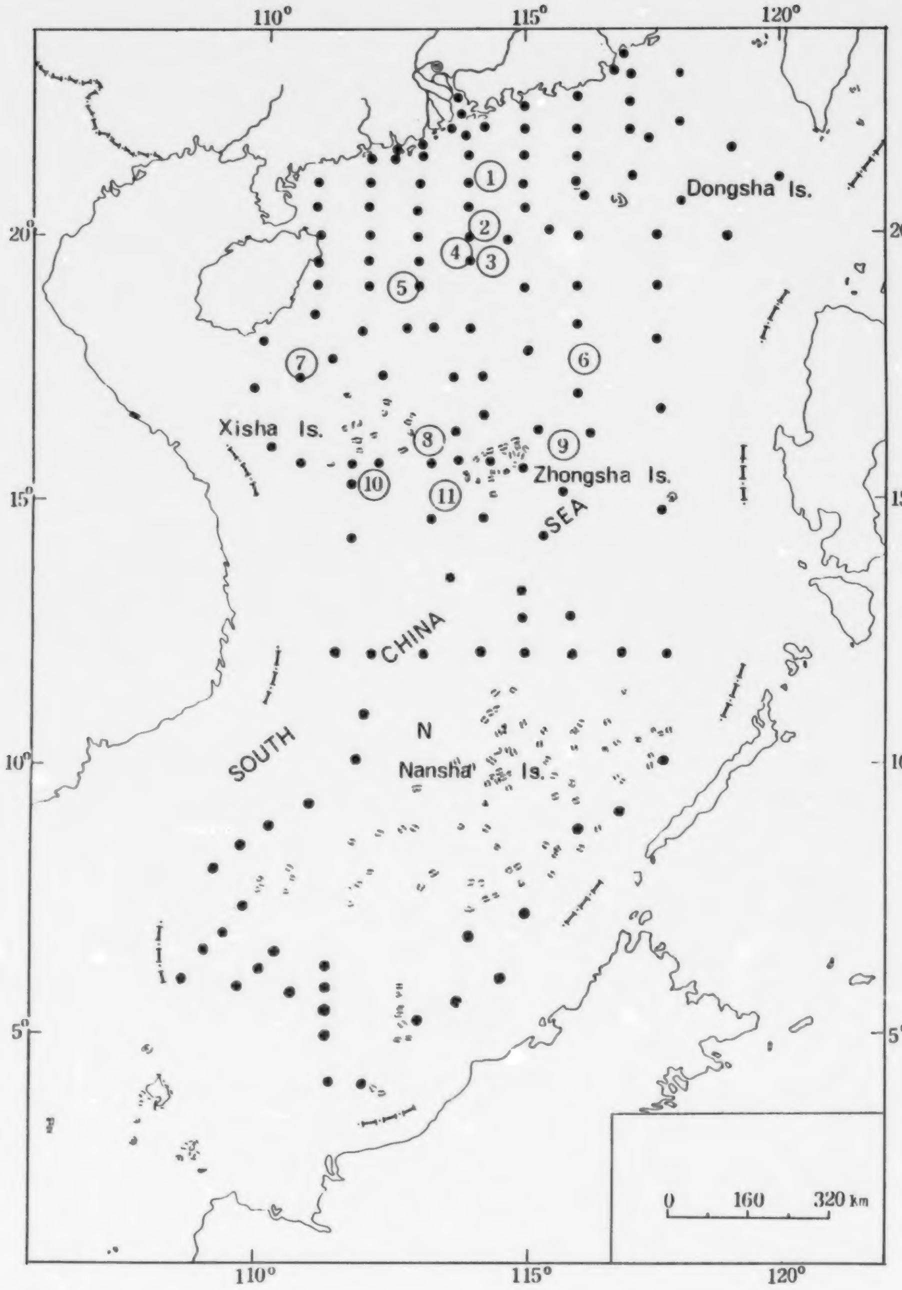

110°
115°
120°
20°
15°
10°
5°
①
②
③
④
⑤
⑥
⑦
⑧
⑨
⑩
⑪
Dongsha Is.
Xisha Is.
Zhongsha Is.
SOUTH
CHINA
SEA
Nansha Is.
0
160
320 km

Figure 1. *Sampling stations from the South China Sea.*
● *Vertical hauls from 200 to 100 m and 100 m to surface layers.*
○ *Vertical hauls from different layers.*

kinds of plankton nets with flow meter attached were used: a conical net with a mouth opening of 80 cm in diameter, length of 230 cm, and mesh size of 15 meshes/cm; a WP-3 net with a mouth opening of 113 cm in diameter, length of 269 cm, and mesh size of 7.5 meshes/cm. Most samples were taken with the conical net. Usually vertical samples from two different layers were taken at each station: 100 m to surface and 200 to 100 m. Samples from deeper waters (e.g., 400 to 200 m and 600 to 400 m) were occasionally collected. Environmental characters, mainly water temperature and salinity, were measured at the surface and on the bottom at each station.

All samples were preserved in 5% formalin. All copepods except some immature specimens were identified to species level. Quantity or abundance of copepods was measured as number of individuals per 100 m^3 of water filtered through the net.

RESULTS AND DISCUSSION

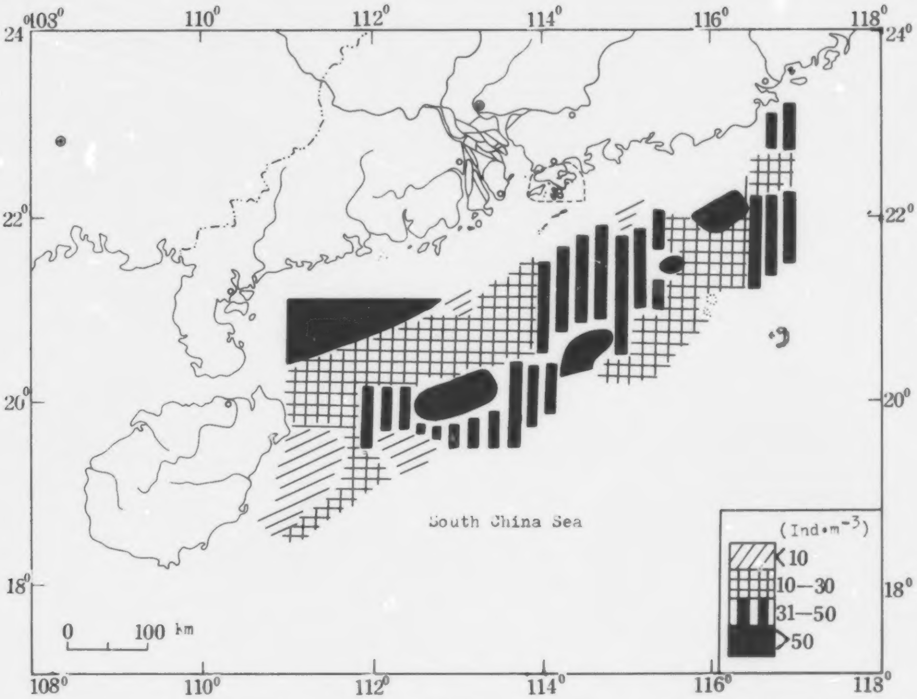
I. Quantitative Horizontal Distribution

The South China Sea is a large marginal sea on the western Pacific. Based on water depth, it is divided into four areas: the estuarine or coastal area (less than 30 m), continental shelf area (30-200 m), continental slope area (200-500 m), and deep sea basin area (more than 500 m).

The number of copepods in our samples in general decreased with the increase of distance from shore (Tab. 1, Figs. 2 and 3). The rate of decrease in abundance also decreased from the estuarine area to the deep sea basin. For instance, the quantity of copepods in estuarine samples was very much higher than that in continental slope samples, and nearly unchanged between the latter and deep sea basin samples. It was noted that occasionally copepods were more abundant in continental shelf samples than in estuarine samples.

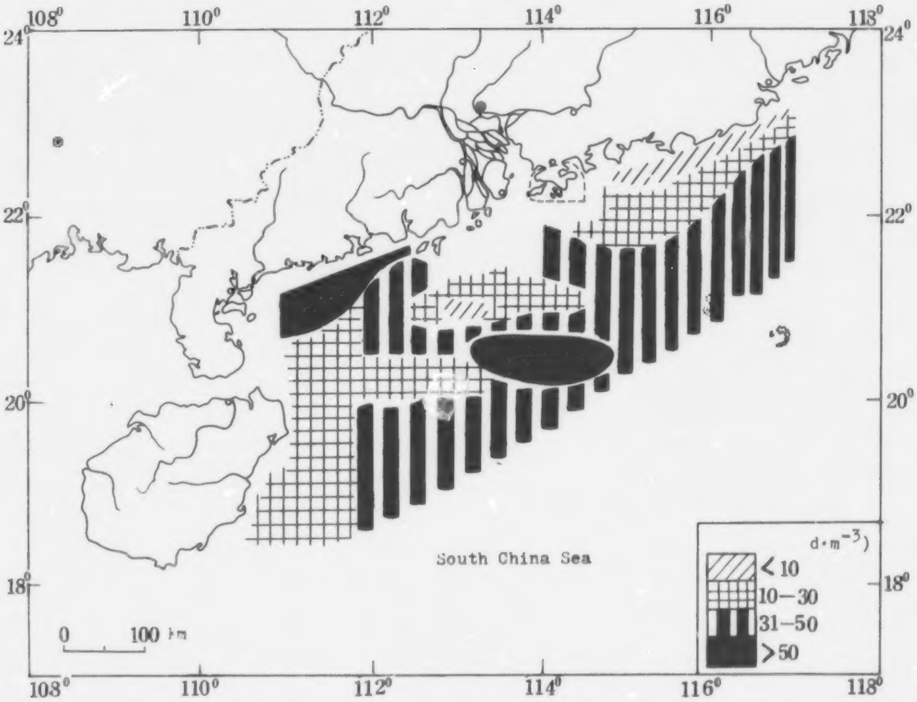
Table 1: *The quantity of Copepoda from the different areas in the South China Sea (Ind. 100 m^3)*

Areas / Months	Estuary and nearshore	The continental shelf			continental slope	The central part of the South China Sea	
		60 m	60-100 m	100-200 m		Zhongsha reefs	Deep-sea basin
1		15785	2639	1713		8525	2040
2		6006	5918	2481		4536	1396
3	24713 (spring)	1720	2045	2349	1022		1603
4		3235	4336	3401	1633	1768	1212
5		2976	3028	3806	629		860
6	49527 (summer)	4065	4300	3587			1406
7		6317	4098	3599	1660		1180
8		5032	3676	2653	1961		
9	87100 (autumn)	2581	7305	2679		2483	1188
10		9571	2929	2676			1299
11		9437	3558	3562			
12	46360 (winter)	4171	1056	3119		3362	958
Means	51925	5908	3741	2969	1381	4135	1314



108°
110°
112°
114°
116°
118°
24°
22°
20°
18°
South China Sea
(Ind•m⁻³)
▨ <10
▦ 10—30
▥ 31—50
■ >50
0 100 km

Figure 2. *The horizontal distribution of the planktonic copepods in the continental shelf area of the South China Sea (May 1978).*



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South China Sea
d•m⁻³)
▨ <10
▦ 10—30
▥ 31—50
■ >50
0 100 km

Figure 3. *The horizontal distribution of planktonic copepods in the continental shelf area of the South China Sea (October 1978).*

2. Quantitative Vertical Distribution

The abundance of copepods decreased from shallow to deep water samples. The decrease was most pronounced between samples taken from 100 m to surface and from 200 to 100 m. The ratio of abundance in samples taken from these two layers is almost 5:1 (Fig. 4).

3. Seasonal Variation in Abundance (Fig. 5)

Seasonal variation in abundance was more noticeable in estuarine waters than in other waters. In the estuarine area of the Pearl and Hanjiang rivers, the greatest abundance of copepods was usually correlated with flood and draught periods. Abundance started to increase in June, reached its peak by early autumn (August), and decreased immediately afterwards.

In nearshore waters of the continental shelf area, the abundance of copepods was greatest in February and July and least in March and December. The ratio of greatest to least abundance of copepods in this area is only 2:1 and is not as obvious as in the estuarine area.

In the offshore waters of the continental shelf area, the abundance of copepods is greatest in summer (May to July) and late autumn (October to November) and least in winter and spring. The difference between the greatest and least abundance of copepods is small (Fig. 5).

The quantity of copepods in continental slope and deep sea basin areas seems to be rather stable throughout the year. In general, the difference in abundance is within the range of 1,000 to 2,000 individuals per 100 m^3.

4. Diurnal Vertical Migration

Pronounced vertical migration was demonstrated in the samples taken from Xianfa Ansha Shoal (16°38'01''N, 116°41'03''E). Most copepods, about 70-80% of the copepod population of the whole water column, occurred in the 50-100 m layer during the day. The center of abundance, with nearly 60% of the copepods in the whole water column, ascended to the upper 0-50 m layer at night (22:00 to 03:00). In the layer of 100-200 m, the concentration of copepods remained relatively stable throughout the day at 15% of the population of the whole water column. Figures 6 and 7 illustrate the abundance of copepods at different depths of different times of day.

At a shallow water station north of Dongsha Island (Pratas Islands) (22°23'00''N, 117°32'00''E), the diurnal vertical migration of copepods is far less significant than that at Xianfa Ansha Shoal mentioned above (Fig. 6). Most copepods were found in the 10-30 m layer (50%) and 30-50 m layer (30%).

5. Copepods as Indicators of Currents

During the northeast monsoon season (October to March), open oceanic water of the Pacific enters the South China Sea through the Bashi Strait between Taiwan and Luzon. The warm water current, Kuroshio, spreads westward to the south of eastern Guangdong Province. A number of tropical species of copepods, including *Euchaeta marina*, *Scolecithrix danae*, *Neocalanus gracilis*, *Pleuromamma gracilis*,

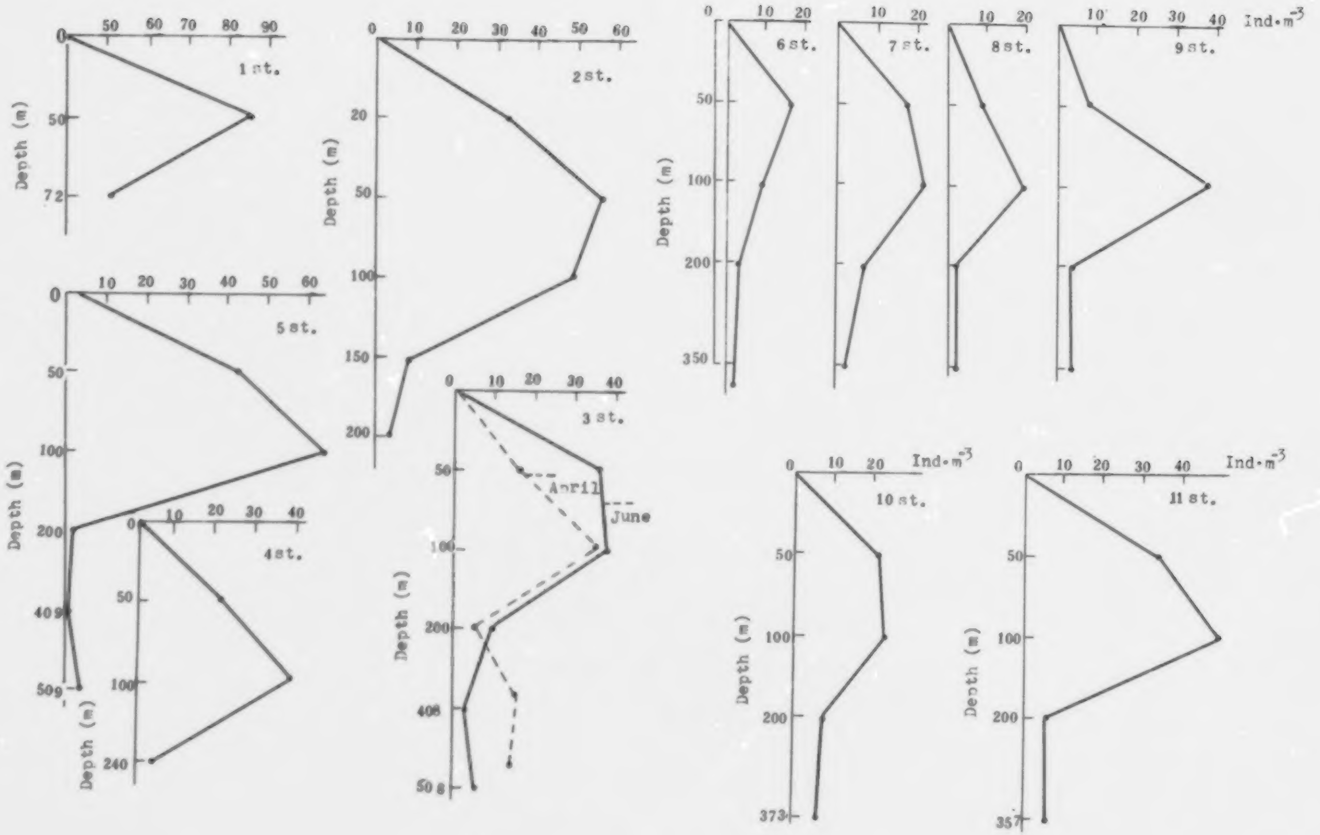

Figure 4 . *The quantitative vertical distribution of copepods of the South China Sea (stations1 to 11).*

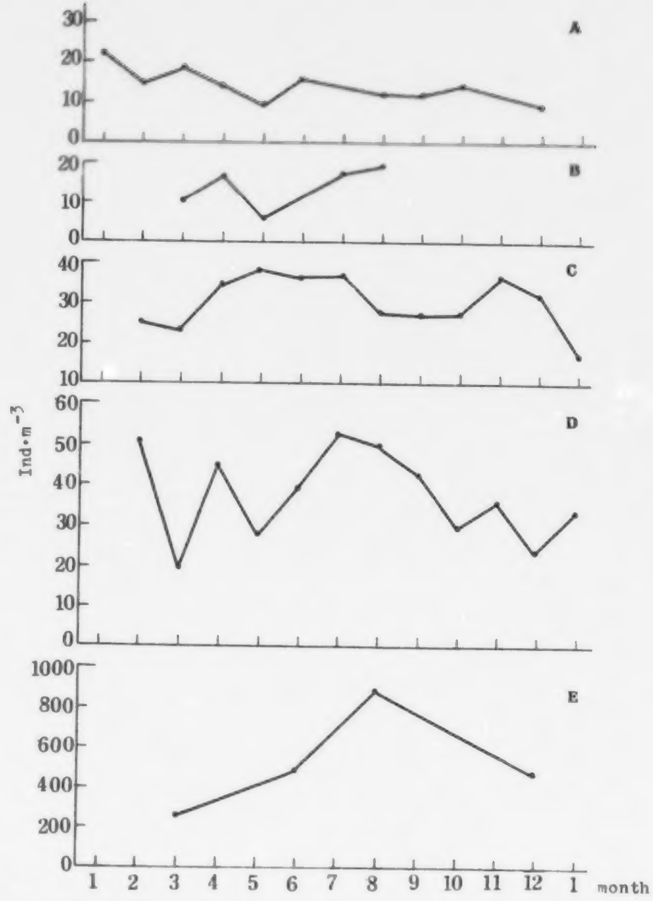

Figure 5. *The sesonal variation in quantity of Copepoda from the different areas of the South China Sea.* **A.** *Deep-sea basin,* **B.** *The continental slope,* **C.** *The offshore waters of the continental shelf,* **D.** *The nearshore waters of the continental shelf,* **E.** *Estuary of Pearl River.*

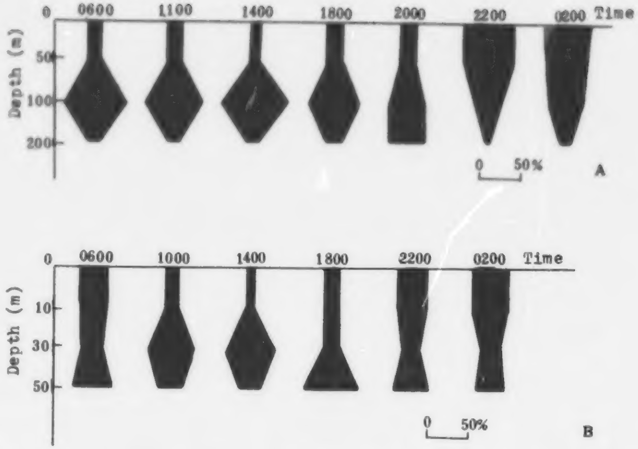

Figure 6. *The diurnal vertical variation of the planktonic Copepoda.*
A. *Xianfa Ansha Shoal ($16^{0}38'01''$N, $116^{0}41'03''$E),*
B. *Pratas Islands ($22^{0}23'00''$N , $117^{0}32'00''$E).*

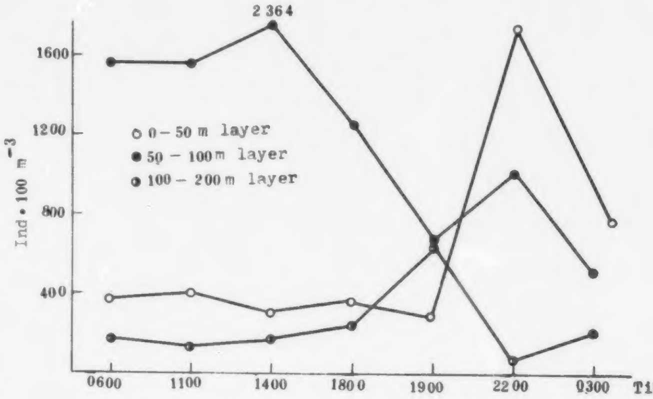

Figure 7. *The diurnal variation of Copepoda from the different layers in Xianfa Ansha Shoal.*

etc., were found close to the continent. In the meantime, a cold water mass moves southward along the coasts of the provinces of Zhejian, Fujien, and Guangdong. Some temperate species of copepods such as Calanus sinicus and Centropages tenuiremis were commonly recorded from the coastal waters of eastern Guangdong Province during the winter and early spring months.

During the southwest monsoon season (May to August), the coastal waters of southern Guangdong Province is freshened by the runoff from Pearl, Hanjiang, and other rivers of the area. Some estuarine species, such as Pseudodiaptomus poplesia, Tortanus gracilis, Acartia erythraea, and Acartiella sinensis, may be found in the surface water over the continental shelf, an indication of the invasion of brackish water.

In the updwelling area southwest of Taiwan, Calanoides carinatus is a good deepwater indicator species.

6. Collection from the Reef Island around Investigator Shoal

Some oceanographic characteristics of the southern part of the South China Sea have been reported by Shirota et al. (1972). The individual numbers of copepods measured as standing crop in this area are 6-10 times less than those in temperate regions. But plankton biomass and phosphate-phosphorus (Po_4-P) contents are high in the coastal area especially near large rivers.

Copepods collected during the survey around the reef islands near Investigator Shoal from June to July 1984 show that the dominant species are Undinula vulgaris, Canthocalanus pauper, Eucalanus subcrassus, Euchaeta concinna, Eucalanus subtenuis, Pleuromamma gracilis, and Rhincalanus cornutus. Some of these species are also found in the northern continental shelf of the South China Sea. In quantitative vertical distribution, we have also found that the maximum abundance of copepods is located in the upper 100 m layer. The vertical abundance and composition of zooplankton is related to the scattering layer in this area as reported by Rolando (1974).

ACKNOWLEDGEMENTS

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LES COPEPODES DES EAUX PORTUAIRES DE MARSEILLE
(Méditerranée nord-occidentale)

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Résumé: L'étude du zooplancton annuel montre que 32 espèces de Copépodes fréquentent les ports. Les plus abondants sont: *Acartia clausi*, *A. discaudata*, *A. latisetosa*, *A. longiremis*, *A. negligens*; *Calanus minor*; *Corycella rostrata*; *Euterpina acutifrons*; *Oithona similis*, *O. nana* et *Paracalanus parvus*. Tout les Copépodes portuaires se retrouvent plus nombreux dans le golfe, exceptés *Acartia clausi* et *Calanus minor*. Les adultes (37% des pêches) s'accomodent mal des eaux polluées étudiées. Les copépodites (48,9% du zooplancton total) sont apparus moins préférentiels et donc moins vulnérables aux effects globaux de la pollution des eaux.

Abstract: A study of the annual zooplankton shows that copepod species inhabit the waters of the harbour of Marseille. The most abundant are: *Acartia clausi*, *A. discaudata*, *A. latisetosa*, *A. longiremis*, *A. negligens*; *Calanus minor*; *Corycella rostrata*; *Euterpina acutifrons*; *Oithona similis*, *O. nana* and *Paracalanus parvus*. All of these are numerically more abundant in the water outside the harbour except *Acartia clausi* and *Calanus minor*. Adults (37% of the total zooplankton) appear more sensitive to polluted water than copepodites (48,9%).

INTRODUCTION

L'intérêt particulier des études sur la pollution globale des eaux (Citarella, 1965, 1972, 1974, 1979) nous a amené à préciser, au sein du zooplancton et plus particulièrement parmi le groupe dominant des Copépodes, quelles étaint les éspèces fréquentant les milieux portuaires du golfe de Marseille ainsi que leur importance et fluctuation annuelle.

Le matériel provient de 66 récoltes effectuées entre les 3 février 1965 et 31 mars 1966 sur 5 stations (Fig. 1). Les traits horizontaux ont été faits avec un filet Juday-Bogorov modifé (Arnaud et Mazza, 1965), à 220 µm de vide de maille, entre 0 et 5 mètres, pendant 10 minutes, à la vitesse de 0.5 ms^{-1}. Sur la moitié aliquote des pêches planctoniques, les Copépodes ont été triés et leur numération ramenée au mètre cube d'eau filtrée.

HYDROLOGIE

Les eaux des stations portuaires (1 et 2) n'ont cessé d'attirer l'attention des écologistes quant à leur impureté croissante depuis les premières observations faites par Marion (1883). Nous avons, en effet, là, un milieu semi-fermé, dont les échanges d'eaux avec le golfe sont essentiellement sous le contrôle des vents dominants et de l'apport des eaux continentales.

Les températures ont fluctué de $8^{o}97$ à $21^{o}60$ ($\pm$ $0^{o}28$) avec une période de réchauffement des eaux (février-octobre) suivie par une période de refroidissement. D' une manière générale la salinité croît avec la profondeur mais s'est montrée très variable (32 à $39^{o}/oo$) Dans l'ensemble, les eaux portuaires se sont révélées plus chaudes et plus diluées.

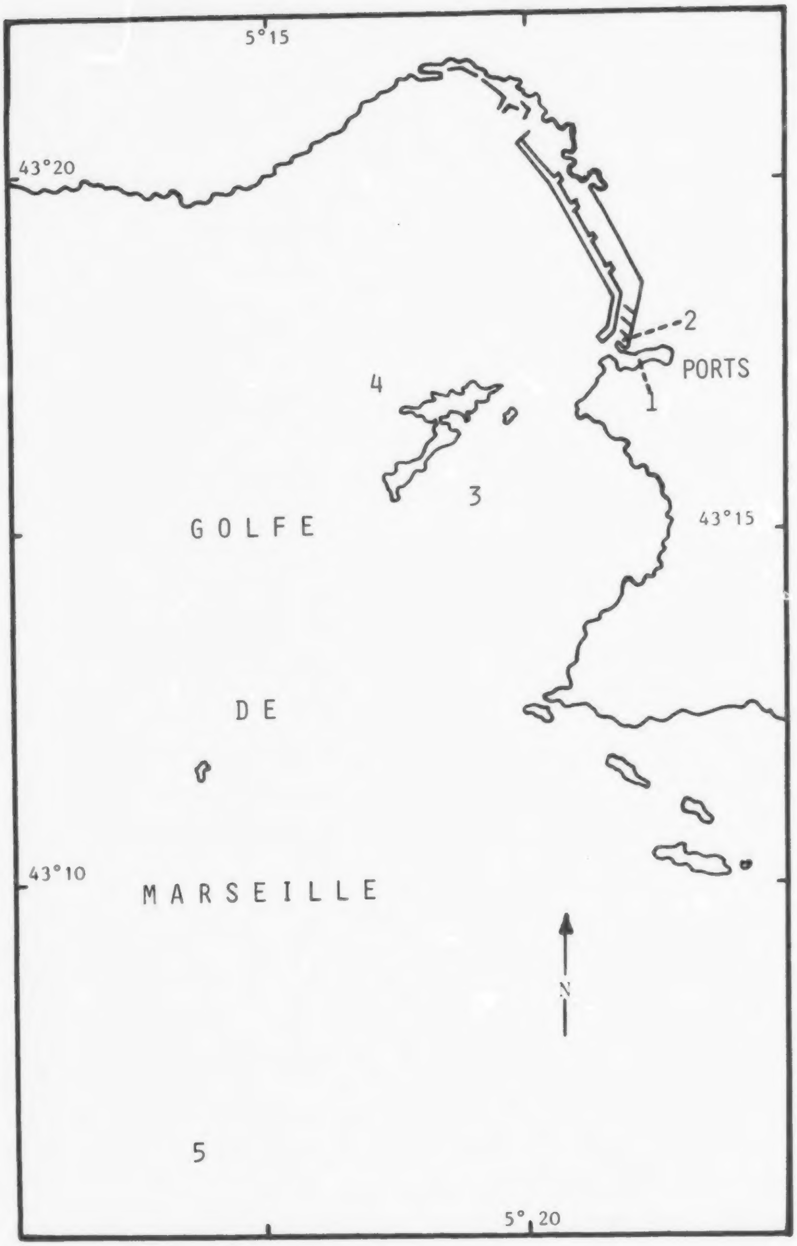
5°15
43°20
2
PORTS
4
1
3
43°15
GOLFE
DE
43°10
MARSEILLE
N
5
5°20

Figure 1. *Répartition des stations d'échantillonnage dans le golfe de Marseille.*

RESULTATS GENERAUX

Dans les ports les Copépodes représentent 85,9% du zooplancton total et parmi eux dominent les copépodites (48,9%).

Trente-deux espèces ont pu être determinées dans nos prélèvements. Elles se répartissent dans les 4 ordres suivants:

CALANOIDA
- Famille des Acartiidae
  - Acartia clausi Giesbrecht, 1889
  - A. discaudata Giesbrecht, 1881
  - A italica Steuer, 1910
  - A. latisetosa Kriczaguin, 1873
  - A. longiremis (Lilljeborg, 1853)
  - A. negligens Dana, 1849
- Famille des Aetideidae
  - Aetideus armatus (Boeck, 1872)
- Famille Calanidae
  - Calanus helgolandicus (Claus, 1863)
  - C. minor Claus, 1863
- Famille des Paracalanidae
  - Paracalanus parvus Claus, 1863
- Famille des Centropagidae
  - Centropages hamatus (Lilljeborg, 1853)
  - C. kröyeri Giesbrecht, 1892
  - C. typicus Kroyer, 1849
- Famille des Euchaetidae
  - Euchaeta hebes Giesbrecht, 1888
- Famille des Temoridae
  - Temora stylifera (Dana, 1849)

CYCLOPOIDA
- Famille des Corycaeidae
  - Corycaeus brehmi Steuer,1910
  - C. clausi Dahl, 1894
  - C. furcifer Claus, 1863
  - C. giesbrechti Dahl, 1894
  - Corycella rostrata Claus, 1863
- Famille des Cyclopinidae
  - Cyclopina litoralis Brady, 1872
- Famille des Oithonidae
  - Oithona nana Giesbrecht, 1892
  - O. similis Claus, 1866
  - Ratania flava Giesbrecht, 1892
- Famille des Oncaeidae
  - Oncaea minuta Giesbrecht, 1892
  - O. notopus Giesbrecht, 1891

HARPACTICOIDA
- Famille des Clytemnestridae
  - Clytemnestra scutellata Dana, 1852
- Famille des Ectinosomidae
  - Microsetella rosea (Dana, 1848)
- Famille des Miracidae
  - Macrosetella gracilis (Dana, 1848)
- Famille des Tachydiidae
  - Euterpina acutifrons Dana, 1852

MONSTRILLOIDA
- Famille des Monstrillidae
  - Cymbasoma longispinosum Bourne, 1890
  - Monstrilla longicornis Thompson, 1890

Toutes ces espèces portuaires ont été retrouvées dans les eaux du golfe de Marseille (St. 3-4 et 5) avec une plus forte densité, excepté pour les 2 Calanoides: Acartia clausi et Calanus minor. Même en tenant compte de la présence de Calocalanus pavo, le 21 février 1978, dans une récolte effectuée à proximité de notre station 2, (Afri et al., 1982); 24 espèces sont absentes dans les ports (Gaudy, 1970) réitérant ainsi les effets léthaux de la pollution des eaux malgré leur relative eutrophie.

La densité moyenne des Copépodes fréquentant les eaux portuaires est faible: 31 ind.m^{-3}; avec un minimum de 11 ind.m^{-3} en juillet et un maximum de 73 ind.m^{-3} courant février.

Les Calanoides représentent à eux seuls 92 % des Copépodes. Le tableau 1 indique la prépondérance d'Acartia clausi sur toutes les autres espèces, et de façon plus générale celle des Acartiidae. On peut constater que 11 espèces occupent 96 % des exemplaires déterminés. Il s'agit, dans l'ordre décroissant, d'Acartia clausi, A. discaudata, A. latisetosa, A. longiremis, A. negligens et Calanus minor, Corycella rostrata, Euterpina acutifrons, Oithona similis, O. nana, Paracalanus parvus. L'examen de la fréquence des différentes espèces montre de faibles valeurs excepté pour Acartia clausi (100%).

Tableau 1: *Résultats quantitatifs généraux des récoltes*

Espèces	**Nb total.m^{-3}**	**Abondance %**	**Fréquence %**
CALANOIDES			
Acartia clausi	178	68	100
A. discaudata	17,1	6,5	10
A. latisetosa	17	6,4	20
A. longiremis	10,2	4	20
A. negligens	7	2,6	20
Calanus minor	7	2,6	20
Paracalanus parvus	2,3	0,8	10
Acartia italica	1,6	0,6	10
Centropages typicus	1,1	0,4	10
Euchaeta hebes	0,5	0,1	10
Aetideus armatus	0,2	0,07	10
Centropages hamatus	0,1	0,03	20
Calanus helgolandicus	0,001	0,0003	10
Centropages kroyeri	0,001	0,0003	10
Temora stylifera	0,001	0,0003	10
CYCLOPOIDES			
Corycella rostrata	5	2	10
Oithona similis	3,5	1	10
O. nana	2,5	0,9	10
Corycaeus clausi	1,5	0,5	20
Cyclopina litoralis	1	0,3	10
Oncaea minuta	0,6	0,2	20
Ratania flava	0,2	0,07	10
Corycaeus furcifer	0,01	0,003	10
C. brehmi	0,001	0,0003	10
C. giesbrechti	0,001	0,0003	10
Oncaea notopus	0,001	0,0003	10
HARPACTICOIDES			
Euterpina acutifrons	4	1	10
Clytemnestra scutellata	1,2	0,4	20
Microsetella rosea	0,2	0,07	10
Macrosetella gracilis	0,001	0,0003	10
MONSTRILLOIDES			
Monstrilla longicornis	0,02	0,007	20
Cymbasoma longispinosum	0,001	0,0003	10

La présence d'Acartia italica, Clytemnestra scutellata, Corycaeus brehmi, Macrosetella gracilis, Oncaea minuta, O. notopus et Ratania flava est tout à fait particulière à la zone portuaire de Marseille.

FLUCTUATIONS SAISONNIERES

Le cycle saisonnier des principaux Copépodes portuaires est résumé sur la figure 2. En hiver, 10 espèces sont présentes: Acartia clausi, A. discaudata, Corycaeus clausi, Aetideus armatus, Oithona similis, Ratania flava, Euterpina acutifrons, Monstrilla longiremis, Corycaeus brehmi et C. kroyeri. Les Acartiidae dominent, notamment Acartia clausi (38 ind.m^{-3}) qui est à son apogée.

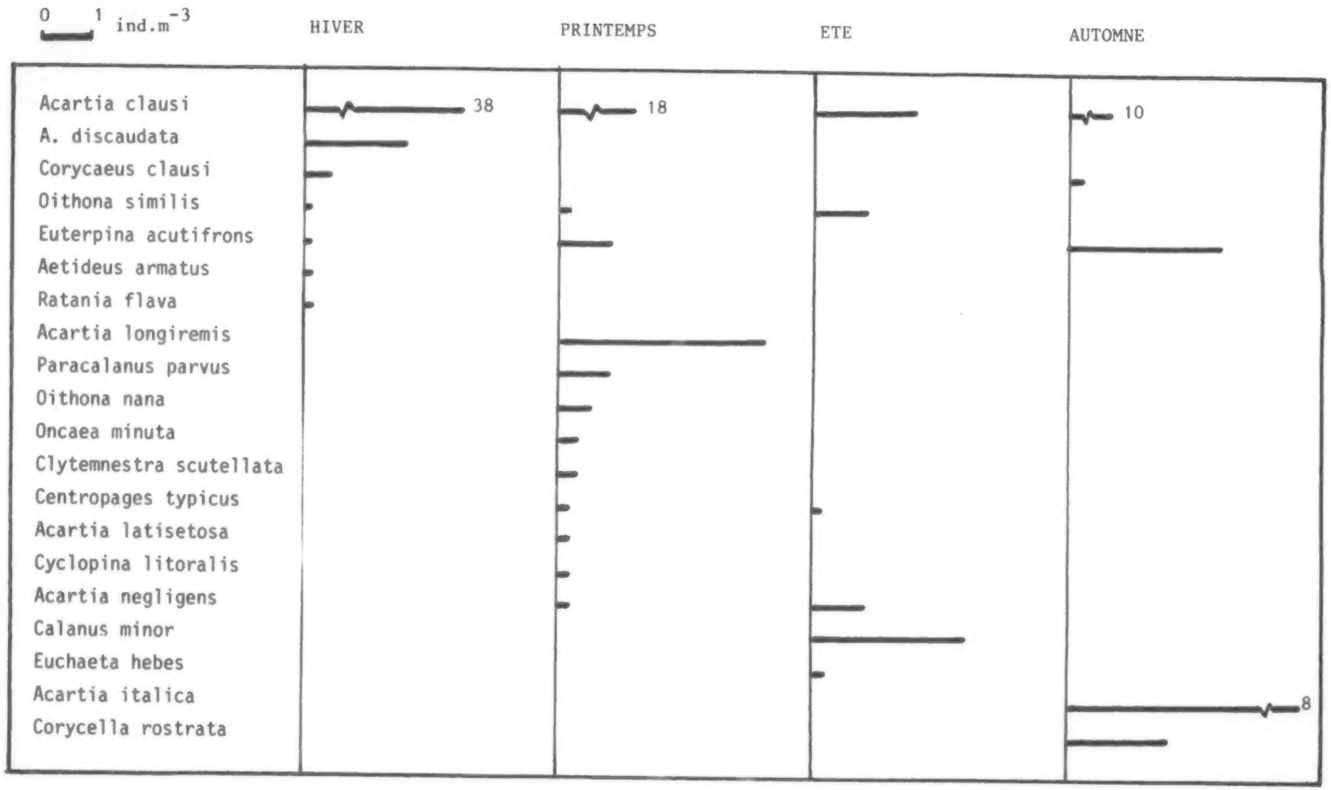

Figure 2. *Distribution saisonnière des principales espèces.*

Acartia discaudata (2 ind.m-3) occupe le 2e rang avec déjà une densité bien réduite. Tous les autres Copépodes comptent moins d'un individu par mètre cube.

Au printemps, la diversité spécifique double (20 espèces). Parmi les Acartia, A. clausi (18 ind.m^{-3}) reste l'espèce dominante, mais Acartia longiremis (4 ind.m^{-3}) remplace Acartia discaudata. Sont remarquables également: Euterpina acutifrons et Paracalanus parvus avec toutes deux un individu par mètre cube. Toutes les autres espèces sont faiblement représentées, par ordre décroissant d'abondance il s'agit de: Oithona nana, Oncaea minuta, Clytemnestra scutellata; Oithona similis, Acartia latisetosa, Centropages typicus, Cyclopina litoralis; Acartia negligens; Euchaeta hebes; Microsetella rosea; Corycaeus clausi; Monstrilla longicornis; Corycaeus furcifer; Calanus helgolandicus, Oncaea notopus et Macrosetella gracilis.

Pendant l'été, 9 espèces ont pu être identifiées mais avec des numérations assez faibles. Parmi les mieux représentées citons: Calanus minor (3 ind.m^{-3}) alors dominante, Acartia clausi (2 ind.m^{-3}) est à son minimum, Oithona similis et Acartia negligens (1 ind.m^{-3}). Centropages typicus et Euchaeta hebes se maintiennent en petit nombre (0,1 ind.m^{-3}). Trois nouveaux Copépodes apparaissent: Acartia italica, Centropages hamatus et Temora stylifera.

Durant l'automne, le nombre d'espèces est réduit à 7. Les plus abondantes sont: Acartia clausi (10 ind.m^{-3}) pérenne, Acartia italica (8 ind.m^{-3}) alors à son maximum ainsi qu'Euterpina acutifrons (3 ind.m^{-3}) et Corycella rostrata (2 ind.m^{-3}) nouvelle. Corycaeus clausi, C. giesbrechti et Cymbasoma longispinosum sont rares.

Chaque saison paraît caractérisée par la présence remarquable d'un Acartiidae. C'est ainsi que, mis à part Acartia clausi, espèce constante dans les eaux portuaires, nous avons relevé:

Acartia discaudata l'hiver,
A. longiremis le printemps,
A. negligens l'été,
et A. italica l'automne.

DISCUSSION ET CONCLUSION

Les milieux portuaires étudiés représentent à la fois une aire eutrophique et polluée où les populations de Copépodes diminuent qualitativement et en nombre. Bien que les copépodites soient relativement abondants au printemps, moins de 50% d'entre eux arriveront au stade adulte. Comme les advections, la prédation joue, dans les ports, un rôle assez réduit. Il semble donc qu'il faille chercher dans le degré de pollution globale des eaux la cause des faibles numérations d'adultes. Acartia clausi apparaît l'espèce la moins gênée par la pollution des eaux au cours de l'année sur les 32 espèces décelées.

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SEX DETERMINATION AND ATYPICAL MALE DEVELOPMENT IN A POECILOSTOMATOID COPEPOD, PSEUDOMYICOLA SPINOSUS (RAFFAELE AND MONTICELLI, 1885)

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Abstract: Pseudomyicola spinosus (Raffaele and Monticelli, 1885), found in Japanese blue mussel, Mytilus edulis galloprovincialis, has six free-swimmng naupliar stages and six infestive copepodid stages. The last copepodid stage is the adult which consists of three forms: atypical male (a slender, small, active swimmer), typical male (a large crawler), and female.

Our **in vitro** experiments on the larval development show that: **1.** sex determination depends largely on the presence of an adult, with a propensity of becoming the opposite sex of the adult present, **2.** sex determination occurs in the second copepodid stage, **3.** larvae develop equally into both sexes when reared alone and in the case of male development almost invariably developing into an atypical male, **4.** the host age and amount of nutrient have no influence on the development of atypical male, and **5.** female egg production is not affected by mating with atypical male.

The life history of Pseudomyicola spinosus (Raffaele and Monticelli, 1885) was recently worked out by Do et al. (in press). According to them, this species of poecilostomatoid copepod has six free-swimming naupliar stages and six infestive copepodid stages, with the last copepodid stage being the adult. Furthermore, three adult forms were recognized by them: atypical male (a slender, small, active swimmer), typical male (a large crawler), and female. The two types of males can be easily obtained by **in vitro** culture, i.e., the atypical male by using isolated culture method, and the typical male by applying congregated culture method. Since factor(s) in sex determination and production of atypical males are still unknown in this poecilostomatoid copepod, we carried out further experiments in an attempt to elucidate the effect of adult presence on the sexual development of the two types of males, and on the egg production resulting from mating with the different types of males.

MATERIAL AND METHODS

The host, Mytilus edulis galloprovincialis, were collected in the littoral zone at Natsushima in Tokyo Bay for the supply of parasites. All experiments were carried out at 30‰ and 20°C. The culture technique described by Do et al. (in press) was used throughout the present experiments.

Fifteen experiments were devised, each of them was carried out either once or twice with 12 or 20 first copepodid larvae. They were reared in isolation with or without an adult as indicated in Table 1. Three kinds of adults were used in testing the production of atypical males: virgin female, postmating female, and mature male. In order to find out the effect of host age and amount of nutrient on the development, the larvae were reared separately on a strip of young host gill (method M in which the host is less than 4 cm long and younger than a year), a strip of old host gill (method N in which the host is more than 4 cm long and older than a year), and a large piece of gill (method O in which the host is about 120 x 40 mm).

Table 1. *Summary of experiments and their results showing the production of atypical male and sex determination under various rearing procedures.*

Experiment	Copepodid stages I II III IV V VI	Adult form	Set 1	Set 2	Total	Sex-ratio
A (with adult ♂)	┗━━┷━━┷━━━━━┛	A♂	0	0	0	0.00%
		T♂	0	0	0	
		♀	18	12	30	100%
B (with virgin ♀)	┗━━┷━━┷━━━━━┛	A♂	0	2	2	100%
		T♂	13	8	21	
		♀	0	0	0	0.00%
C (with mated ♀)	┗━━┷━━┷━━━━━┛	A♂	2	4	6	96.55%
		T♂	9	13	22	
		♀	0	1	1	3.45%
D (without adult)	└───────────┘	A♂	4	5	9	45.00%
		T♂	0	0	0	
		♀	6	5	11	55.00%
E (with adult ♂)	┗━━┷────────┘	A♂	7		7	52.94%
		T♂	2		2	
		♀	8		8	47.06%
F (with adult ♂)	┗━━┷━━┷─────┘	A♂	1	0	1	3.23%
		T♂	0	0	0	
		♀	18	12	30	96.77%
G (with adult ♂)	└──┴━━┷━━━━━┛	A♂	0		0	0.00%
		T♂	0		0	
		♀	10		10	100%
H (with adult ♂)	└──┴──┴━━━━━┛	A♂	4		4	58.33%
		T♂	3		3	
		♀	5		5	41.67%
I (with mated ♀)	┗━━┷────────┘	A♂	8		8	50.00%
		T♂	0		0	
		♀	8		8	50.00%
J (with mated ♀)	┗━━┷━━┷─────┘	A♂	15		15	84.21%
		T♂	1		1	
		♀	3		3	15.79%
K (with mated ♀)	└──┴━━┷━━━━━┛	A♂	5	5	10	96.29%
		T♂	13	3	16	
		♀	1	0	1	3.71%
L (with mated ♀)	└──┴──┴━━━━━┛	A♂	7	2	9	63.33%
		T♂	4	6	10	
		♀	7	4	11	36.67%
M (on young host)	└───────────┘	A♂	10	12	22	62.85%
		T♂	0	0	0	
		♀	6	7	13	37.15%
N (on old host)	└───────────┘	A♂	7	7	14	39.50%
		T♂	0	1	1	
		♀	10	13	23	60.50%
O (on large gill)	└───────────┘	A♂	7		7	40.00%
		T♂	1		1	
		♀	12		12	60.00%

Note: Thick line indicates stages reared with the presence of adults and thin line, without. A♂: atypical male; T♂: typical male.

RESULTS

I. Effect of adult presence on the development of larvae:

In experiment D, the larvae reared in isolation without accompaniment of adults developed almost equally into both sexes, and in the case of the male, it is represented solely by the atypical male. However, when the larvae were reared in the presence of adult females, regardless of virgin or postmating (experiments B and C), they developed largely into a male population - 100% with the virgin female and 96.55% with the postmating female. Furthermore, the males were represented chiefly by the typical male - 91.3% with the virgin female and 75.57% with the postmating female. Interestingly, when the first infestive copepodid larva was reared with a mature male (experiment A), it invariably developed into a female.

II. Determination of sex during larval development:

The larvae developed into the opposite sex when their second copepodid stage was spent together with an adult. In experiments E and H, when larvae were not reared in the presence of an adult male during their critical second copepodid stage, nearly equal numbers of either sex were obtained. However, when an adult male was present at this critical stage (experiments F and G), almost all of the larvae developed into females. Similar results were obtained when the adult male was placed with a postmating female (in experiments I and L).

III. Effect of host age and nutrient value on larval development:

Experiments M, N, and O clearly show that the development of atypical males is not affected by the host age nor by the amount of nutrient. The results are comparable with experiment D, where both sexes were obtained with a significantly high possibility of atypical male production.

IV. Reproductive ability of atypical male:

Ten atypical males, another 10 typical males and 20 virgin females obtained respectively from experiments B, C, and D were used to test the reproductive ability of the atypical male. Each female paired with one of either kind of male was reared separately in a small Petri dish. Each pair was continuously observed for six months, from May to November, 1983.

Between 10 to 22 (17.3 in average) pairs of egg sacs were produced by the female-typical male pair and 9 to 25 (17.6 in average) by the female-atypical male pair. The female produced in these six months an average of 233.5 eggs by pairing with a typical male and 233.3 eggs by pairing with an atypical male. The average numbers of eggs deposited in a sac at each egg laying for the first 22 times of egg production are shown in Figure 1. The results show similar reproductive ability of both kinds of males.

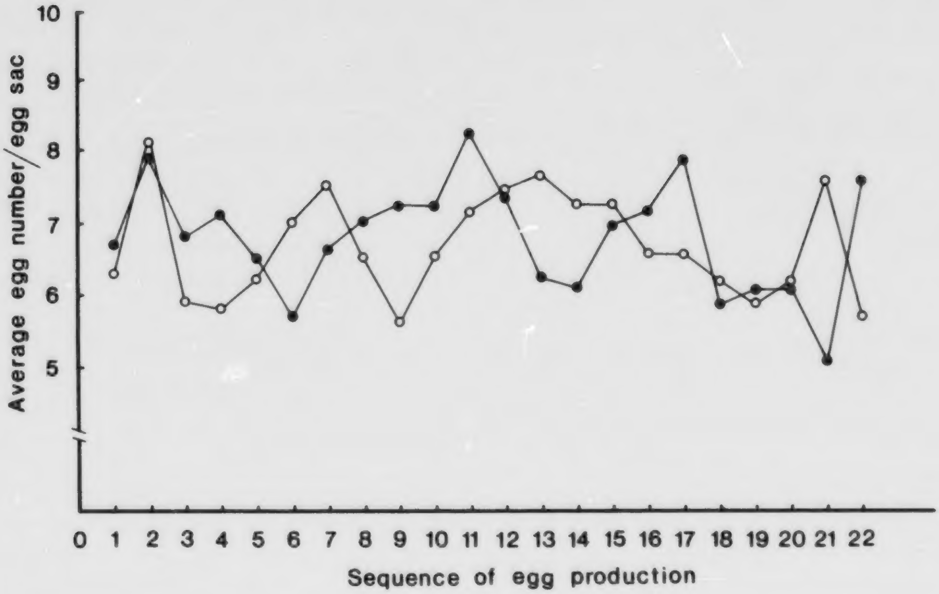

Figure 1. *Egg production for six months in 10 females mating with atypical males (O———O) and another 10 females mating with typical males (●——●).*

DISCUSSION

Ginsburger-Vogel and Charniaux-Cotton (1982) reported that Copepoda (presumably free-living) are gonochoric with their sex determination controlled by a polygenic mechanism and epigenetic factors, such as inbreeding and temperature.

It is particularly interesting to note that in the case of a symbiotic copepod, Pachypygus gibber (Thorell), an endosymbiont living in the pharyngeal cavity of the ascidian, Ciona intestinalis (Linnaeus), the sex determination depends largely on the age of the host (Hipeau-Jacquotte, 1978). In young hosts, the larvae grow up into an atypical male and in older hosts they develop mostly into a female. Therefore, host age seems to be the determining factor for the production of atypical male in this parasitic cyclopoid copepod.

The development of an atypical male described by Do et al (in press) for Pseudomyicola spinosus seems to be controlled by other kinds of factor. As indicated by experiments D, M, N, and O, the development of an atypical male in P. spinosus is due to isolation and not the host age. Experiments A, B, and C clearly show that P. spinosus is another example of epigenetic sex determination as reported by Ginsburger-Vogel and Charniaux-Cotton (1982). But what from the adult copepod is the actual determining factor of the larval sexual development?

Sex pheromone of some females of free-living copepods is known to induce mating behaviour (Katona, 1973, Griffiths and Frost, 1976). Our experiments A, F, and G show that the adult male of P. spinosus induces development of females and similarly, in experiments B, C, J and K, that the adult female promotes the development of males. Therefore, we hypothesize that in P. spinosus the adult of both sexes is capable of producing something like a "sex-determining pheromone" to induce the development of the other sex. Furthermore, this "sex-determining pheromone" is only effective during the second copepodid stage of larval development, if it is received before (in experiments E and I) or after (in experiments H and L) this critical stage, the effect is minimized. As elucidated by Do et al. (in press), isolation is the chief mechanism in the development of an atypical male in P. spinosus. Comparison between experiments J and K corroborates this finding. The critical second copepodid stage was exposed to "sex-determining pheromone" in both experiments, but when these copepod larvae were reared to adults with the continuous presence of an adult female (in experiment K), their chance of becoming an atypical male was reduced to 38.5%, whereas under isolated conditions (in experiment J), it was maintained as high as 93.8%. In other words, the factor that affects the production of an atypical male is independ of the sex-determining factor.

ACKNOWLEDGEMENTS

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THE MESOCYCLOPS SPECIES PROBLEM TODAY

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INTRODUCTION

Mesocyclops occurs everywhere except the Arctic Tundra and the Antarctic. It is especially common in the tropics, where it is the predominant crustacean carnivore (Fernando, 1980). Its role in mosquito egg and larval predation is being evaluated. (Rivière 1984). Till very recently, one species, Mesocyclops leuckarti (Claus) described in 1857 from Germany was considered cosmopolitan. It held a status similar to Chydorus sphaericus. Kiefer (1981) showed that it is restricted to Europe and Western Asia. Kiefer's (1981) study and the subsequent work of Dussart (1982, 1984) and Van de Velde (1984) has firmly established Mesocyclops species diagnosis.

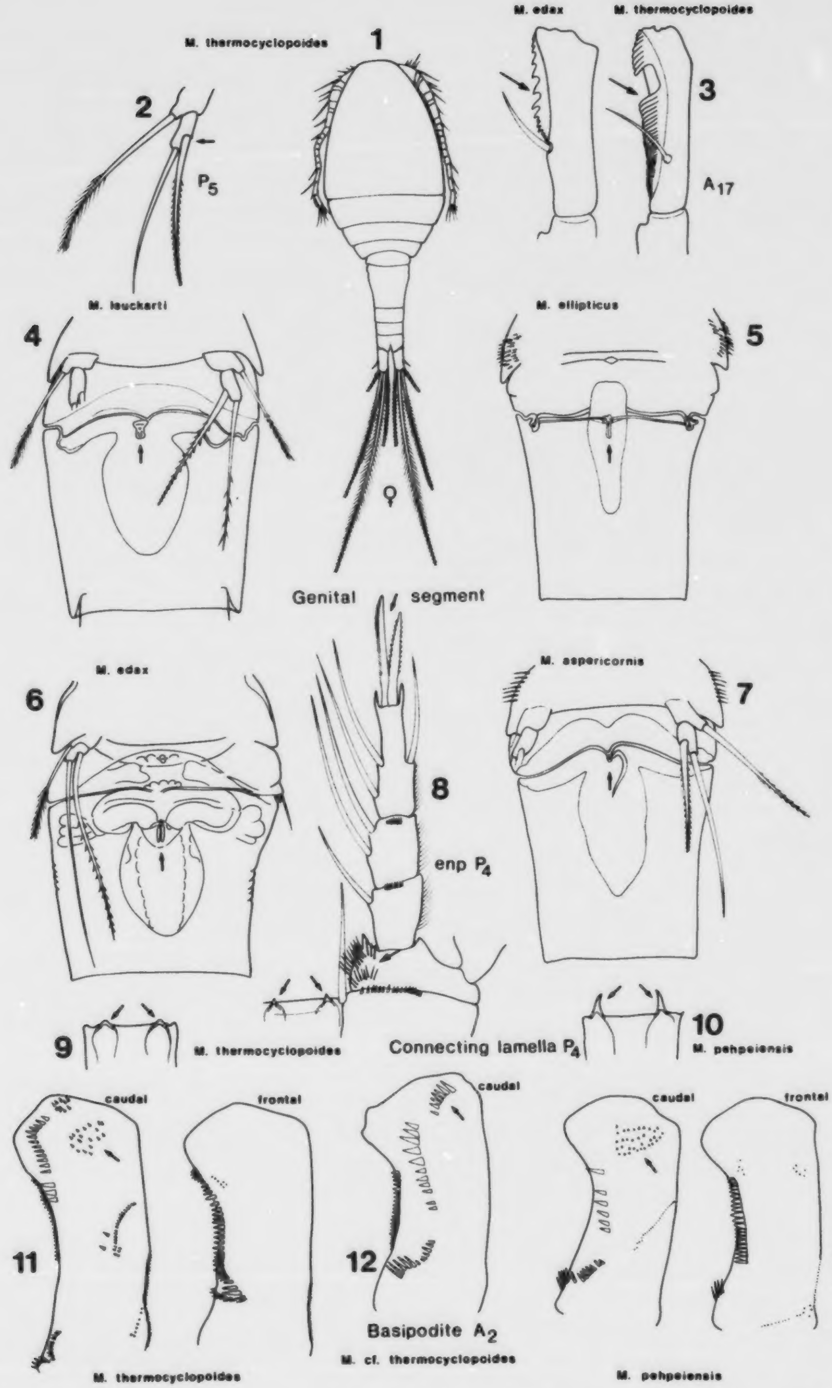
Recent systematic studies of other zooplankton groups, the Cladocera (Frey 1980, 1982) and Rotifera (Dumont 1983), has shown that the uncritical acceptance of widespread cosmopolitanism was common but mistaken. A similar situation has existed in the cyclopoid Copepoda. We know now that many Cyclopoida species reported earlier as cosmopolitan from freshwaters have a restricted distribution.

Rotifera show the phenomenon of anabiosis and are predominently parthenogenetic. These features favour dispersal. The Cladocera are facultative, more rarely obligate, parthenogenetic forms. This favours their dispersal. Copepoda are sexually reproducing forms and therefore species should have a more restricted distribution. This scale of cosmopolitanism would only apply of other relevant factors to dispersal and survival are equivalent for the three groups. The cosmopolitanism of Cyclopoida was considered an anomaly. Recent systematic studies indicate that this anomaly was only apparent.

In this paper we are presenting an overview of the genus Mesocyclops focussing on the historical growth of our taxonomic knowledge since Mesocyclops leuckarti, the first member of the genus, was described about 125 years ago. We have also added data on the occurrence of species in Asia, Australia and America where misidentification or lack of data is greatest. We have listed the known species and commented on their zoogeography.

MATERIALS AND METHODS

The pertinent literature on the systematics and distribution of Mesocyclops globally was critically examined to provide an overview. A list of presently known species and their distribution was compiled. Some gaps in distribution are filled by an examination of material available to us from Australasia, Asia and America.


M. thermocyclopoides
1
M. edax
M. thermocyclopoides
2
P5
3
A17
M. leuckarti
4
M. ellipticus
5
♀
Genital segment
M. edax
6
M. aspericornis
7
8
enp P4
9
M. thermocyclopoides
Connecting lamella P4
10
M. pehpeiensis
caudal
frontal
caudal
caudal
frontal
11
12
13
Basipodite A2
M. thermocyclopoides
M. cf. thermocyclopoides
M. pehpeiensis

Figs. 1-13. *Some features used in genus and species diagnosis of Mesocyclops. **1:** General facies. **2:** P_5 showing different levels of insertion of inner setae. **3:** Hyaline membrane of A 17 (M. edax is not typical). **4-7:** Details of RS. **8:** P_4 showing endopodite, coxal lamella and chaetotaxy of basipodite **8-9:** Coxal lamella of the same species showing variation **10:** Coxal lamella of another species showing consistant feature **11-12:** Basipodite of A_2 of two very closely related species or the same species **13:** Another species showing differences in chaetotaxy. (Arrows indicate diagnostic features).*

THE GENUS MESOCYCLOPS

Mesocyclops is presently a well defined genus. It is characterised by, among other features, a prominent hyaline membrane, on segment 17 of A_1, P_5 with a two segmented base and three spines of which the two inner ones are inserted at distinctly different levels and P_4 with a characteristic connecting lamella bearing prominences (Fig. 1,3,8-10). Mesocyclops is more inclined to carnivory than its most closely related genus Thermocyclops from which it differs in the nature of the insertion of the two inner spines of P_5. Earlier systematists based their species diagnoses on many features including the hyaline membrane of segment 17 of A_1 which were nevertheless considered variable (Gurney 1933). Features like the nature of the prominences on the connecting lamella of P_4, the relative sizes of the terminal spines of the endopodite of P_4, the presence of hairs on the inner side of the furca were also used, but inconsistantly. Kiefer (1981) relied on the detailed structure of the receptaculum seminis (Figs. 4-7) and Van de Velde (1984) uses this feature and the chaetotaxy of the basipodite of A_2 (Figs. 11-13) in species diagnosis besides of course a number of other features.

NOTES ON HISTORY

The history of our knowledge of the taxonomy of Mesocyclops illustrates the impact of general scientific (or intuitive) ideas on conclusions reached in systematics.

The earliest reference to the genus Mesocyclops is the description of Mesocyclops leuckarti (Claus) in 1857 from Germany. The subsequent literature on the genus is almost exclusively European until the end of the nineteenth century when two species, one each from North and South America, M. edax (Forbes, 1891) and M. annulatus (Wierzejski, 1892) were described.

The European Mesocyclops leuckarti was generally considered cosmopolitan until the publication of Kiefer's (1981) paper on the old world members of the genus. Eighteen species belonging to the genus had however, been described in the century before Kiefer's (1981) work. Gurney (1933) did more than any other author to consolidate the view that M. leuckarti was cosmopolitan. He had some doubts about its occurrence only in South America. Other workers including Kiefer whose work on Copepoda spans the period 1923-present* accepted the cosmopolitanism of M. leuckarti in keeping with the generally held view.

It is certain that some species remain to be described (Table 1). It is also possible that some African, Asian and American species are synonyms, though this is less likely. At the present time the least explored areas for Mesocyclops are the Australasian and American, and to a slightly less extent Asian continents. We have attempted to fill this gap by the examination of material available to us from these regions. The presently known distribution of the species is listed in Table 1.

NEW RECORDS

We examined some of the material available to us from Asia, Australia and America. -A list of species we found and the localities are given in Table 1.

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* KIEFER died on 17. April 1985

Table 1. *The occurrence of Mesocyclops species globally. Listing is broadly by continents and in order of first description.*

A. Presently known distribution of *Mesocyclops*

Africa - (including Malagasy)
M. aspericornis, *M. major*, *M. aequatorialis*, *M. annae*, *M. pilosus*, *M. thermocyclopoides* s.l. (?), *M. paludosus*, *M. ogunnus*, *M. salinus*, *M. rarus*, *M. kieferi*, *M. dussarti*, *M. spinosus*

America:

North of Mexico-*M. edax*, *M.* spp.

South - *M. annulatus*, *M. aspericornis* s.l., *M. longisetus*, *M. meridianus*, *M. brasilianus*, *M. ellipticus*

Central and Caribbean - *M. edax*, *M. longisetus*, *M. brasilianus*, *M. ellipticus*, *M. nicaraguensis*

Asia - *M. leuckarti*, *M. aspericornis*, *M. annae*, *M. thermocyclopoides*, *M. tobae*, *M. rectus*, *M. petroeiensis*, *M. mongoliensis*, *M. microlasius*

Australasia - *M. aspericornis* (Papua New Guinea), *M. notius*, *M. thermocyclopoides* (N.S.W. and Vic.)

Europe - *M. leuckarti*, *M. thermocyclopoides*

B. New records (present authors) of *Mesocyclops*

America

North of Mexico - *M. longisetus* (Florida), *M. sp.* (Most of North America)*

Central and Caribbean - *M. meridianus*, *M. thermocyclopoides* s.l.

Asia - *M.*** *aspericornis* (Kalimanatan, Sulawesi, Sabah, Sarawak, Burma, Sri Lanka), *M. thermocyclopoides* (Kalimatan, Nepal, Sulawesi), *M. annae* (Sri Lanka), *M. pehpeiensis*, (Burma, Sri Lanka, Malaysia)

Australasia - *M. annae* (N.T. Queensland), *M. thermocyclopoides* (S.A., N.T., W.A., Queensland), *M. notius* (S.A., N.T. Queensland), *M. rarus* (N.T.), *M. pehpeiensis* (N.T.)

Undescribed species - M. sp. (Most of North America)* M. sp. (Rangoon, Burma) M.sp. (Faisalabad, Pakistan)

ZOOGEOGRAPHY

The distribution of old world species has been documented by Kiefer (1981) and Van de Velde (1984). The presently known distribution is given in Table 1. There appear to be two cosmotropical species, *M. aspericornis* and *M. cf. thermocyclopoides*. Van de Velde (1984) has cast doubt on the occurrence of *M. thermocyclopoides* in Africa. Dr. Richard Lim, Kuala Lumpur, Malaysia found that in Asia there are at least two species very closely related to *M. thermocyclopoides* (Figs. 11 and 12) Van de Velde (personal communication) agrees with this view. The occurrence of *M. aspericornis* in America needs confirmation. Some species like *M. pehpeiensis* and *M. thermocyclopoides*, *M. annae* and *M. leuckarti* have a wide latitudinal distribution. We found two African species *M. rarus* and *M. annae* in Australia. North America has besides *M. edax*, at least two species *M. longisetus*, and one or more species recorded as *M. "leuckarti"* previously.

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* which will be called *M. americanus* (Dussart, 1985).

** Kiefer (personal communication) stated that *M. thermocyclopoides* is probably found only in China, Vietnam and Burma.

SUMMARY

The taxonomy of the widespread genus *Mesocyclops* was poorly known till 1981. The European species *Mesocyclops leuckarti* was considered cosmopolitan. It is now known to be restricted to Europe and Western Asia. About 30 species of the genus, mainly from tropical and subtropical regions are now well documented. The concept of widespread cosmopolitanism in freshwater microcrustaceous has been responsible for the uncritical acceptance of the worldwide distribution of well known European species like *M. leuckarti* and *Chydorus sphaericus*. As more and more material from the tropics becomes available the extent of cosmopolitanism can be assessed. Critical taxonomic studies of these groups outside Europe are very badly needed for such an assessment.

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MESOCYCLOPS AND *THERMOCYCLOPS* POPULATIONS IN LAKE KINNERET (ISRAEL)

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Abstract: The seasonal distribution of *Mesocyclops ogunnus* (= *M. leuckarti*; *M. thermocyclopoides*) (Van de Velde) and *Thermocyclops dybowskii* (Lande) in Lake Kinneret was studied during 1975-1983. Seasonal fluctucations of population densities, of both species are relatively stable throughout the year. The relative abundance of *M. ogunnus* during the period 1979-1983 was lower than during 1975-1978. Development time of *T. dybowskii* was experimentally measured at 15°C. It was found that males of both species developed at similar rate but duration time of females of *M. ogunnus* was longer. Body size of *T. dybowskii* is smaller than that of *M. ogunnus*. It is suggested that intensification of fish predation pressure was the reason for increasing relative abundance of the small *T. dybowskii*.

INTRODUCTION

The relative abundance and/or competition between cyclopoid genera or species in freshwater lakes of different geographic regions was studied by many authors (Hutchinson, 1967). The Old World *Cyclops* genus is mostly common in Europe but in tropical and subtropical regions, or in temperate latitudes in summer, *Cyclops* is replaced by *Mesocyclops* and *Thermocyclops* (Hutchinson, 1967).

The close genera *Mesocyclops* and *Thermocyclops* have in many lakes similar ecological characteristics as well as similar size when they co-occur. *Mesocyclops* is commonly associated with *Thermocyclops* (Hutchinson, 1967). The dominant cylopoid copepods in the plankton of Lake Kinneret are *Mesocyclops ogunnus* (*M. leuckarti*; *M. thermocyclopoides*) (Kiefer, 1981; Van de Velde, 1984) and *Thermocyclops dybowskii* (Gophen, 1978, 1984). The co-occurrence of *M. ogunnus* and *T. dybowskii* in Lake Kinneret was previously documented by Richard (1893), Gurney (1913), Boodenheimer (1935), Yashouv and Alhunis (1961). Intensive studies of the zooplankton of Lake Kinneret indicate multiannual changes of relative abundance of these two species. In the present paper the co-occurrence and multiannual fluctuations of *M. ogunnus* and *T. dybowskii* are considered.

METHODS

Monitoring of adult *Thermocyclops* and *Mesocyclops* in Lake Kinneret was carried out on a weekly basis. The nauplii and 1-4 copepodite stages were not separately recorded in routine samples. The monitoring procedures are given in Gophen (1978, 1984). Culturing techniques of *T. dybowskii* for the determination of life stages durations are given in Gophen (1976). The biomass of adult organisms of *Mesocyclops* and *Thermocyclops* are given in Gophen (1973, 1976, 1977).

RESULTS AND DISCUSSION

Since the nauplii and 1-4 copepodite stages of T. dybowskii and those of M. ogunnus were not routinely monitored separately, densities presented in Table 1 are those of adults. The biomass of adult females of M. ogunnus was found to be significantly bigger than that of females of T. dybowskii (22.4 $\mu g_{(w.w.)}$ and 9.2 $\mu g_{(w.w.)}$ respectively) whilst males were not significantly different (Gophen, 1973, and unpubl. data).

Table 1. *Monthly averages of adult (males and females) densities (No. l^{-1}) of* M. ogunnus *and* T. dybowskii *in two periods: 1975-1978 and 1979-1983; standard deviations varied between 10-30%. The relative abundance (%) and multiannual averages ($\bar{x}$) ($\pm$ S.D.) are given.*

Month	M. ogunnus				T. dybowskii			
	1975 - 1978		1979 - 1983		1975 - 1978		1979 - 1983	
	No. l^{-1}	%	No. l^{-1}	%	No. l^{-1}	%	No. l^{-1}	%
1	9	82	11	73	2	18	4	27
2	13	81	13	81	3	19	3	29
3	11	65	6	67	6	35	3	33
4	8	80	3	60	2	20	2	40
5	9	90	4	50	1	10	4	50
6	11	91	8	73	1	9	3	27
7	11	100	7	88	0	0	1	12
8	12	92	9	69	1	8	4	31
9	9	100	4	57	0	0	3	43
10	10	100	7	70	0	0	3	30
11	11	91	5	63	1	9	3	37
12	11	82	6	67	2	18	3	33
$\bar{x}$ ($\pm$ S.D.)	10 (1)	88 (10)	7 (3)	68 (10)	2 (2)	12 (10)	3 (1)	33 (10)

Life stage durations were measured experimentally. Experiments were carried out at $15^{o}C$. Mated egg carrying females were seperated into 15 ml filtered lake water individually. Immediately after hatching the females were removed and nauplii were cultured to adulthood and daily observed (Gophen, 1976). Twenty-five cultured organisms were matured. Results of development times are presented in Table 2. It is likey that at $15^{o}C$ life stages durations of M. ogunnus and T. dybowskii are similar. Results in Table 2 also indicate that in both species, the development time of males was shorter than that of females. Assuming similar relative durations at higher temperatures, these two species have a rather high degree of similarity in their life cycle development time. On the other hand, as previously mentioned, body size of adult females of T. dybowskii is smaller than that of M. ogunnus (Gophen, 1973).

Table 2. *Duration times of nauplii and copepodite instars, in days (± S.D.) of T. dybowskii and M. ogunnus (Gophen, 1976). Total and population averages are given.*

	M. ogunnus		T. dybowskii	
	Male	**Female**	**Male**	**Female**
Nauplii	25 (8)	28 (10)	35 (3)	35 (3)
Copepodites	27 (2)	39 (0.4)	18 (1)	22.5 (4)
Total	52	67	53	57
Population average	60		55	

It is suggested that the predation pressure of visual particulate attacking zooplanktivorous fish on adult females of M. ogunnus is higher than that of the smaller females of T. dybowskii (Drenner et al., 1982). Drenner et al. (1982) documented a negative index of selectivity of particulate feeding by S. galilaeus on copepodites 1-4 and a high positive value on copepodite 5, and adults of M. ogunnus. The body size of adult T. dybowskii is much smaller than copepodite 5 and adults of M. ogunnus, i.e. capture probability of adult M. ogunnus is higher than that of T. dybowskii.

Seasonal distribution

Results in Table 1 represent significant (95% confidence limit) reduction of the relative abundance of M. ogunnus during the period of 1979-1983 in comparison with previous years. Results in Table 1 show also that seasonal changes of the abundance of the adults are very minor for both species.

It was previously documented that during recent years in Lake Kinneret, fish predation pressure, mostly visual particulate feeders (bleaks), and cichlid fingerlings, on zooplankton was intensified (Spataru and Gophen, 1985; Landau, 1984; Gophen and Pollingher, in press; Gophen, 1984; Gophen et al., 1983a, b). The predation pressure on zooplankton by fish was mostly pronounced during spring-summer-fall period. I suggest that the reduction of relative abundance of M. ogunnus and increase of respective values of T. dybowskii are mostly due to intensification of fish predation. This pressure is relatively more efficient on larger organisms (M. ogunnus) than on smaller ones (T. dybowskii) (Drenner et al., 1982). This suggestion is based, among others, on the assumption of similarity in life cycle durations of both species. The impact of the relatively low temperatures during winter season (January-March) is reduction of fish predation pressure on zooplankton. Consequently increasing of densities of M. ogunnus and T. dybowskii populations is expected. Nevertheless the low winter temperatures affect cyclopoids development time to be longer than in other seasons (Gophen, 1976), therefore, population densities are not increasing. In other words, the relatively low mortality (=predation) of cyclopoids is accompanied by their low productivity and their densities are not higher than in other months when fish predation pressure is more intensive.

Interspecific relations between M. leuckarti, T. hyalinus, and C. vicinus in the plankton of Norfolk Broads were observed by Gurney (1933). He pointed out that they co-occurred and with a size scale gradient: C. vicinus > M. leuckarti > T. haylinus. Hutchinson (1967) described similar limnetic co-occurence elsewhere between large M. leuckarti and small M. tobae; large T. hyalinus and small endemic T. woltereckij and the benthic forms of large Eucyclops parvicornis and small E. agilis (=serrulatus). Kiefer (1933; 1938) documented similar co-occurrence of T. hyalinus and T. decipiens, in Southeastern Asian lakes, where T. decipiens was slightly smaller. In other lakes where these two species had similar sizes they exclude each other in the plankton. The smaller T. crassus and the larger M. leuckarti, were described as the only two cyclopoid species dominated and co-occurring in the limnetic zooplankton of Sri-Lanka (Fernando, 1980).

It can be concluded that when two freshwater cyclopoid genera and/or species co-occur, in most cases there is a body size difference between them. The existence of a dominant size gradient, when two different sized freshwater cyclopoids co-occur, from North to the tropical latitudes can be suggested; large sized cyclopoids dominate in northern regions and vice versa in the tropics. What are the ecological factors which cause such a phenomenon? It can be suggested that, due to the increased temperature gradient and the reduction of seasonal temperature fluctuations (i.e. relative increase of winter temperatures) from north latitudes to the tropics, the total annual food requirements of freshwater fish become higher. In other words, fish predation pressure gradient on freshwater zooplankton is increasing along the gradient from north to the tropics. Therefore, zooplankton community structure response is predomination of small size cyclopoids. The advantage of such a size structure is increased escapability and consequently survival. Other factors affecting the production of small size cyclopoids in the tropics like food availability or metabolic balances may also be important but are not considered in this paper.

I suggest that both species, small T. dybowskii and large M. ogunnus co-existed in Lake Kinneret with the dominance of the latter due to ecological adaptations including fish predation pressure which was lower than the present (Gophen, 1976, 1977). Inverse relations between two cyclopoids, small T. hyalinus and large M. leuckarti were documented by Burgis et al. (1973) in tropical Lake George. In Lake George the small T. hyalinus is dominant whilst large M. leuckarti and cladocerans produce a minor part of zooplankton biomass. It was concluded by Burgis et al. (1973) that these relativ densities were caused by intensive predation pressure of Chaoborus and zooplanktivorous fingerlings. Intensification of zooplanktivorous fish predation pressure in Lake Kinneret has slightly modified the size structure of the ecosystem and resulted in general reduction of zooplankton biomass (Gophen, 1984; Gophen and Pollingher, 1984) by lowering the relative abundance of large cladoceran (Gophen, 1983) and copepod (M. ogunnus) populations as presented here. This sequence of events was similar to that described by Brooks and Dodson (1965). The implication of such a process in Lake Kinneret is deteriorating water quality (Gophen et al., 1983a, b; Gophen and Pollingher, 1984). The following citation is relevant to the present Kinneret conditions: "It is worth determining whether changes in size structure can provide an early warning about deteriorating lake quality" (Sprules, 1980). My answer based on the Kinneret data record, is yes!

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POSSIBLE POLYMORPHISM IN THE NUDIBRANCH-INFESTING LICHOMOLGID COPEPOD DORIDICOLA AGILIS LEYDIG

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Abstract: Small numbers of ovigerous females of Doridicola agilis from three nudibranch host species obtained at four localities in British and Irish waters have been measured. Some differences are apparent in overall size as well as in the form and length/breadth ratio of the fifth leg. Tentative conclusions are drawn as to whether this situation is host influenced or is dependent on geographical and ecological factors.

Doridicola agilis Leydig, 1853, is a cyclopoid copepod of the family Lichomolgidae which occurs as an ecto-associate of nudibranch molluscs. About 30 species of the latter have been recorded as hosts and, in addition, a tectibranch, a polychaete and, possibly, a cephalopod have been reported to harbour this versatile associate. It has been found in the Mediterranean, on the Atlantic coasts of Europe and Africa from Scandinavia to Senegal, and in the western north Atlantic on the Canadian Coast.

Boxshall and Platts (1978) in recording it from Aeolidiella sanguinea (Norman) and Archidoris pseudoargus (Rapp) collected in the same locality on the Donegal coast of western Ireland, observed some small differences in the form and proportions of the reduced fifth leg. Specimens from A. pseudoargus had a marked proximal expansion on the inner margin of the free segment, and the two apical setae were about equal in length. The length/maximum breadth ratio of this leg was 3.06. Individuals from A. sanguinea possessed only a slight proximal expansion, the inner apical seta was distinctly longer than the outer, and the fifth leg was 3.49 times longer than its greatest width. On this basis, Boxshall and Platts suggested that D. agilis could well be a plolymorphic species.

Small collections of this copepod from four localities in British and Irish waters and from three species of nudibranch hosts were made available to me a few years ago, through the kindness of Mrs Elizabeth Platts and Dr. Chris Todd. Some measurements of overall size were taken before the specimens were used as experimental material for testing various techniques aimed at removing surface débris prior to scanning electron microscopy. Subsequent to these treatments (which reduced the numbers still further) the fifth legs of representatives from each collection were examined and measured. The results, which extend the initial observations of Boxshall and Platts, are given in table 1 below. All the copepods measured were adult females, and all but two were ovigerous.

Clearly the number of specimens available for detailed study is too small to be statistically significant. The results, however, suggest that larger collections from more localities and additional nudibranch host species, might shed some light on interesting but barely understood aspects of intraspecific variation in associated copepods. Even from the scanty data presently to hand, we can perhaps tentatively infer the following:

1. D. agilis would indeed seem to be polymorphic, at least as regards the form and proportions of the fifth leg, and probably as regards overall length as well.

2. The evidence to date does not suggest that we are dealing with a geographically influenced cline.
3. It would appear difficult to correlate the observed variation with the nudibranch species infested. For example, specimens from *Jorunna tomentosa* in Jersey are, on average, the largest, whilst those from the same host collected in Co. Clare are the smallest.

Table 1

Host	Locality	Number of of copepods measured	Average length in mm	Size range in mm	Fifth leg 1/b ratio
Archidoris pseudoargus	Jersey	2	0.91	0.89-0.92	3.62
Archidoris pseudoargus	Anglesey	6	0.95	0.87-1.02	2.30
Archidoris pseudoargus	Donegal	-	-	-	3.06*
Aeolidiella sanguinea	Donegal	2	1.01	0.94-1.08	3.46
Jorunna tomentosa	Jersey	5	1.05	0.99-1.07	3.43
Jorunna tomentosa	Clare	5	0.77	0.56-0.90	5.10

*Data from Boxshall and Platts (1978)

Since geographic location and direct host influence do not, at present, seem to be significant factors, can we draw any valid conclusions as to the genesis and maintenance of polymorphism in this cyclopoid? If we consider the fifth leg l/b ratios, two populations at once appear anomalous - that infesting *A. pseudoargus* at Anglesey, and the specimens associated with *J. tomentosa* on the Clare coast. Omitting these, we might reasonable postulate that an "average" mature female would be expected to have a fifth leg l/b ratio of about 3.40, with anything between, say, 3.00 and 3.70 constituting a "normal" and insignificant fluctuation. The copepods from Anglesey and Clare, however, possess ratios which are respectively well below and markedly above this range.

The present author has not seen any of the collection sites involved, but some information on them has kindly been supplied by Mrs. Platts, who investigated the Clare, Donegal and Jersey areas, and by Dr. Todd who collected the Anglesey specimens. The Clare site (Finavarra) is an inlet off Galway bay, and provides more sheltered environment than the Donegal locality (St. John's Point and nearby Murles Point). In particular, it would seem that at Finavarra water exchange with neighbouring areas is likely to be limited. The Channel Islands site (La Rocque, Jersey), although topographically sheltered, is subjected to very large tides and strong currents which probably ensure extensive mixing with adjacent water masses. The Anglesey location (Church Island, Menai Strait) is rather similar to Clare in affording a small area of limited water exchange potential. It is conceivable, therefore, that in Anglesey and Clare we have sites in which the planktonic larval stages of *D. agilis* have relatively little opportunity for dispersal beyond the confines of their hatching area. Unfortunately we know nothing regarding the duration of the planktonic phase in the life cycle of this copepod. However, Lönning and Vader (1984) have provided some data on the young stages of certain *Doridicola* species infesting sea-anemones on the Californian coast. They believe that infection of the host may take place during the first copepod instar, in which case the planktonic (dispersive) phase is restricted to naupliar stages of limited locomotory ability and probably lasting no more than 10-14 days. It may be suggested, then, that the conditions prevailing at the Clare and Anglesey sites would promote the establishment and maintenance of essentially local and relatively isolated populations of *D. agilis*. There is considerable evidence that it is under such circumstances that small mutations, probably of no adaptive significance, can become fixed within a limited gene-pool.

It should perhaps be emphasized yet again that this hypothesis is not only speculative, but is based on extremely scanty data. However, *Doridicola agilis* is a widespread and abundant species, asssociated with a great variety of hosts, and is relatively easy to obtain. Further studies are therefore well worthwhile.

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COPEPODS IN ARCTIC SEA ICE

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Abstract: At least 12 species of copepods, including 5 harpacticoids, 3 cyclopoids, 3 calanoids and one monstrilloid, have been found inhabiting the annual sea ice in Frobisher Bay, in the eastern Canadian Arctic. The cyclopoid *Cyclopina* sp. was the most numerous. Other abundant species included the harpacticoids *Tisbe furcata*, *Harpacticus superflexus* and *Halectinosoma* sp. *Cyclopina*, represented by eggs, nauplii and all copepodid stages, appeared to undergo reproduction and development within the ice. At least 90% of copepods were found in the lower 20 cm of the ice, most in the lower 3 cm. Harpacticoids and cyclopoids, rare in the plankton, comprised most of the copepod fauna in the ice. Calanoids, overwhelmingly dominant in the plankton, were extremely uncommon in the ice. The ability to feed on the abundant diatoms and to adapt to the high salinity and low temperature of the brine channels in the ice are two of the major qualifications for prolonged sea ice habitation.

INTRODUCTION

The sea ice of the Arctic consists of the so-called permanent pack of the Arctic Ocean and the temporary or annual ice of the peripheral seas. The temporary ice differs from the permanent pack in that it breaks into small units as melting proceeds and either drifts away from its point of origin or melts in place, leaving the water surface ice free until the next winter's ice growth begins. Arctic ice meiofauna studies, including the present one, have been carried out only in the temporary ice in which biota is re-established annually.

During growth, sea ice loses salt, and in the process brine channels are formed, opening to the sea through the lower surface (Lake and Lewis, 1970). Concentrated brine from the ice and sea water from beneath the ice have been found in the channels (Tsurikov, 1980). It appears that the ice fauna also inhabits the channels.

Across the arctic the ice fauna is abundant and diverse, and includes at least 30 species of several major taxa, including ciliates, nematodes, polychaetes, rotifers, amphipods, a variety of larvae of benthic species, and copepods (Grainger et al., 1985). The copepods are the best represented group taxonomically, and at least 16 species have been found to date (Table 1; including additional data from Cross, 1982; Carey and Montagna, 1982, and Kern and Carey, 1983).

The present study was carried out in Frobisher Bay (about 63°43'N, 68°31''W) in the eastern Canadian Arctic. The plants of the ice were investigated by S.I.C. Hsiao, of the Arctic Biological Station, who found a microalgal flora of 227 species, dominated by 213 species of diatoms (Grainger and Hsiao, 1982). Hsiao showed that the standing stock increased as the ice grew in thickness, ranging from 10^6 to 10^7 cells per m^2 in February and March to more than 10^9 cells per m^2 in June, that cells were far more abundant in the lower 5 cm than higher in the ice, and that cell concentrations in the ice exceeded those of the phytoplankton in the water beneath the ice by 7 to 72 times, and especially in late winter and spring appeared to provide a significantly more concentrated nutrient source for herbivorous copepods than existed at the same time in the water below.

Table 1. *Copepods reported from the sea ice of the Arctic*

Calanoida

Acartia longiremis (Lilljeborg)*
Calanus sp.*
Pseudocalanus sp.*

Cyclopoida

Cyclopina gracilis Claus*
Cyclopina schneideri Scott*
Cyclopina sp.*
Oithona similis Claus*
Oncaea borealis G.O. Sars
Oncaea minuta Giesbrecht

Harpacticoida

Dactylopodia signata (Willey)
Dactylopodia vulgaris (G.O. Sars)*
Halectinosoma finmarchicumScott*
Halectinosoma neglectum G.O. Sars*
Harpacticus superflexus Willey*
Harpacticus uniremis Kroyer*
Microsetella sp.
Pseudobradya sp.
Tisbe furcata (Baird)*

Monstrilloida

Monstrilla sp.*

*Found in the ice in Frobisher Bay

METHODS

Cores of about 7.2 cm diameter, obtained with a SIPRE ice corer, supplied most of the collections described here. Holes of 60-90 cm in diameter were dug manually from the surface to about 15 cm from the bottom of the ice. The remaining ice was then carefully extracted from each hole and retrieved with minimal disturbance to its lower surface, from which additional samples were taken.

At first, only the lower 3 cm of the ice were retained for examination. Later, the lower 20 cm were collected, and later still, 20 cm levels were added through much of the length of the cores. The melted ice and contents were filtered through nylon mesh (73 μm at the start of the study, later 10 μm, to minimize loss of organisms much smaller than copepods). Animals were identified and counted, and recorded numerically and as wet weight per m^2 of surface. At the time of ice sampling, zooplankton was collected from the total water column beneath the ice, using a 73 μm mesh hauled vertically.

RESULTS

Three species accounted for more than 90% of the copepods taken in the ice in Frobisher Bay. Most numerous was an unidentified cyclopoid, referred to tentatively as Cyclopina sp., then came the harpacticoids Tisbe furcata and Harpacticus superflexus.

Cyclopina sp.

There were two species of this genus expected in the ice: C. schneideri and C. gracilis, both found in our collections in the plankton of Frobisher Bay and both reported in the sea ice elsewhere (Cross, 1982; Cross and Martin, 1983; Kern and Carey, 1983). These two species were found in small numbers in the Frobisher ice, but the dominant representative of the family in the ice was another, as yet unidentified species.

Numbers collected on 4 dates in 1981 in the lower 3 cm of ice and in the water below the ice are shown in Fig. 1. Numerous in the ice in February, they disappeared from the ice by mid-June. Numbers were small in the water beneath the ice until June, when they rose abruptly.

Early copepodids dominated in the ice in February and March (Fig. 2). Older stages increased in May, by which time adult females were the most numerous stage. During the winter, individuals in the water beneath the ice were too few to permit assessment of stage frequencies. By June, when the species had left the ice, numbers had risen in the water, where most stages were represented.

The large majority of eggs taken in the ice belonged to Cyclopina sp. This was the only copepod found carrying eggs in the ice, and the species to which all but a very few of the stage I copepodids in the ice belonged.

Four ice samples were collected in March and May to assess numbers of animals occurring at various levels in the ice sheet. About 80% of the Cyclopina were taken in the lower 3 cm, and a total of about 90% were found in the lower 20 cm. The remaining 10% were in levels 20-40 cm and 40-60 cm from the bottom of the ice, and all stages were included.

Tisbe furcata

The genus is reported from sea ice in the Antarctic (Andriashev, 1968) and (as furcata) in the Arctic (Cross, 1982). Numbers barely exceeded 300 per m^2 in the ice in March and were lower at other times in 1981 (Fig. 1). Fewer were found in the ice than in the water below through the season. Early copepodids were relatively rare both in the ice and in the water (Fig. 2). There was no clear evidence of seasonal development through copepodid stages in the ice. No eggs belonging to the species were identified in the ice.

In the March and May samples taken to determine the spread of animals through the ice, the lower 3 cm contained about 75% of all the Tisbe, the lower 20 cm more than 90%. Older copepodids, including mainly adult females with fewer males and stage V, dominated above the lower 3 cm in March and May.

Harpacticus superflexus

Total numbers in the collections were small, both from the ice and the water beneath it. In February, only adult females were taken, in the ice and the water. In March, some copepodid stages I and II were found in the ice and by May all but stage I were collected there. Stages V and VI were domninant by May, and total numbers were highest in the ice - up to 800 per m^2. By June, stages V and VI appear to have abandoned the ice for the water. The species was not found at any time above the lower 3 cm of the ice.

Other species

All other copepods were far less numerous in the ice than the 3 species already discussed. Of particular interest was the occurrence of the cyclopoid Oithona similis, and the only calanoids taken in the ice, Acartia longiremis, Calanus glacialis and Pseudocalanus sp. These are the major planktonic

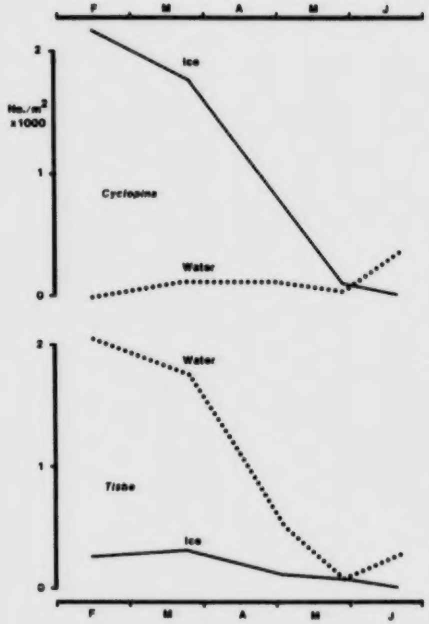

Figure 1. *Numbers of Cyclopina and Tisbe in the lower 3 cm of the ice and in the water below the ice from February until June of 1981.*

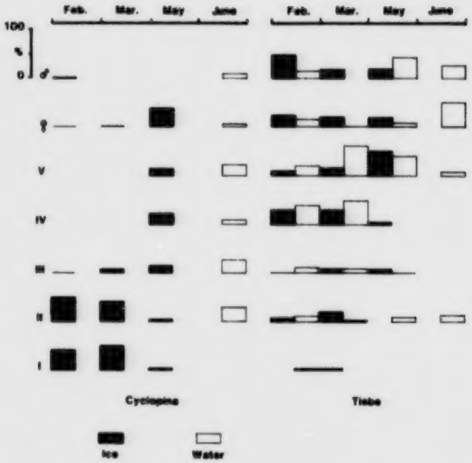

Figure 2. *Percentages of copepodid stages of Cyclopina and Tisbe in the lower 3 cm of the ice and in the water below the ice between February and June.*

species of the area. Very abundant under the ice, Acartia was found only once in the ice, as 5 individuals per m², at a time when there were some 5000 per m² in the water below the ice. Similar differences between ice and water were found in the other three species.

DISCUSSION

The lower few centimentres of sea ice support a substantial meiofauna (Grainger et al., 1985), and the copepods are one of the principle groups included. Cyclopina sp., the most abundant ice inhabitant of the group, was consistently far more numerous in the ice, where it appeared to complete much of its life cycle, than in the water below. Tisbe, the second ranking copepod numerically in the ice, nevertheless remained primarily an inhabitant of the water below. It is interesting, therefore, that these two genera, along with Harpacticus, have been reported elsewhere as being primarily benthic, although having some ability to live planktonically as well (Ceccerelli, 1976; Hauspie and Polk, 1973). The other major copepod group, the calanoids, dominant planktonically throughout the year, formed almost no part of the ice fauna, and they, of course, are known widely as a holoplanktonic group.

Two of the principal adaptations of copepods to ice habitation appear to be concerned with feeding and salinity tolerance. To occupy the ice, animals must have access to it and be small enough to enter the channels. For sustained occupancy, they are expected to feed within the ice, presumably on diatoms or other organic particles of small enough size. Feeding mechanisms must be suited to the special restrictions of the ice habitat.

Use of the ice flora as food by the ice meiofauna and the role of both in a longer food chain were suggested first by Andriashev (1968), who referred to the consumption of ice diatoms by copepods and their use in turn by predatory zooplankton and fishes. Later, Horner and Alexander (1972) found several taxa in the ice meiofauna of northern Alaska, and stated (p.455) that: "The...copepods were feeding on ice organisms...". Microalgae were conspicuously present in the lower part of the Frobisher Bay ice from February until breakup in spring, and more plentiful in the ice than in the water immediately below by at least 2 orders of magnitude until the phytoplankton bloom began (Table 2). A potential concentrated food source was therefore indicated, and its utilization was apparent from the number of diatom-filled digestive tracts found in the copepods collected in the ice. Further work on copepod feeding in the ice is currently under way in our laboratory.

Table 2. *Temperature, salinity and chlorophyll a at the bottom of the ice and in the adjacent water. Data from Lovrity (1982) and Grainger and Hsiao (1982).*

	Feb.	**Mar.**	**May**	**June**
Water temperature under ice (°C)	-1.8	-1.8	-1.7	-0.1
Water salinity under ice (%o)	33.5	-	32.9	7.5
Lower ice microalgae (cells x 10^4/L)	286.9	846.5	1342.0	648.9
Surface water microalgae (cells x 10^4/L)	1.1	1.0	0.5	195.9

Most recorded salinity values from sea ice are calculated from melted ice blocks and average around 4%o (Pounder, 1965). Because the salts are not evenly dispersed through the ice but concentrated in brine channels, such total salinity values tell us little about conditions directly affecting the ice biota. From the relationship brine volume (%) $\approx -5.5S$ (‰)/T($^{\circ}$C) (Untersteiner, 1966), where S = salinity derived from melted ice and T = temperature interpolated from measurements made just above and below the ice, brine salinity may be roughly calculated. In this way, approximate salinity and temperature values in brine channels at various levels in the ice may be derived (Table 3).

Table 3. *Calculated brine salinity and temperature at 3 and at 20 cm from the bottom of the ice (from data in Lovrity, 1982, 1984).*

	1981				**1982**		**1983**
	Feb.	**Mar.**	**May**	**Jun.**	**Mar.**	**May**	**Mar.**
Ice thickness (cm)	123	142	142	137	141	159	142
Brine salinity 3 cm in ice (‰)	44	36	31	3	40	29	40
Temperature 3 cm in ice ($^{\circ}$C)	-2.4	-2.0	-1.7	0.0	-2.2	-1.6	-2.2
Brine salinity 20 cm in ice (‰)	101	51	33	0-17	80	22	83
Temperature 20 cm in ice ($^{\circ}$C)	-5.6	-2.8	-1.8	0.4	-4.4	-1.5	-4.6

There are a few isolated measurements in the literature which show observed brine concentrations. Alexander et al. (1974) reported salinity as high as 34‰ in interstitial water in sea ice. Values as high as 72‰ were noted by Zukov (1943; reported by Grant and Horner, 1976). Lewis and Milne (1977) found concentrated brine with salinity as high as 68‰ extruded from brine channels beneath the ice. Tolerance to comparably high salinity is indicated for animals occupying the ice (Table 3) where there would appear to be a need to adapt to a greater range of salinity than in the water (Table 2).

Diatoms have been shown to live and grow under salinity conditions found in brine channels. Grant and Horner (1976) measured salinity tolerance of 4 species of ice-inhabiting diatoms, 2 at least of which have been found in the ice in Frobisher Bay. All 4 showed good growth between 10 and 50‰, one or two of the species growing at as high a salinity as 60‰ and as low as 5‰. Among animals, the copepod Tisbe has been shown (Finney, 1979) to maintain normal movements intertidally at a salinity as high as 45‰.

We are still largely uninformed about the depth of penetration of mobile animals much farther than 3 cm into the ice. The persistence of a fluid state in the brine cells during the coldest period of winter is dependent upon high salinity. In February, for instance, a salinity of 50‰ may have existed around 5 cm from the bottom of the ice, 70‰ near 10 cm from the bottom. It is very improbable that many animals could have maintained normal activity still farther from the water-ice interface at that time. By March, 50‰ salinity may have been as far as 20 cm from the bottom of the ice, and by May all values through the ice were lower than 50‰. Conditions clearly supported the gradual increase in depth of penetration of copepods into the ice from below as air temperatures rose in the late winter. With the beginning of the period of ice melting, however, most of the remaining salt was lost from the ice, brine channels were developed to their maximum extent, and a freshened water layer was formed beneath the ice, flooding the ice channels. It appears that at that time the copepods and other animals retreated from the ice to the waters below.

ACKNOWLEDGEMENTS

We thank J.E. Lovrity, Daphne Ponbtbriand, Lysanne Daoust and Vidar Neuhof for their activities on the ice and in the laboratory, André Theriault for the facilities of the Ikaluit Research Laboratory at Forbisher Bay, and Esso Resources Canada Limited and Canterra Energy Limited for financial support.

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VERTICAL DISTRIBUTION OF COPEPODS IN THE EURASIAN PART OF THE NANSEN BASIN, ARCTIC OCEAN*

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Abstract: During the Swedish Arctic expedition YMER-80 to the Eurasian part of the Nansen Basin and the shelf areas north and northeast of Svalbard, a total of 58 samples was taken by vertical, fractionated hauls at 23 different stations from $78^{\circ}58'$N to $82^{\circ}32'$N and $14^{\circ}51'$E to $45^{\circ}54'$E.

Twenty three species of copepods were identified. The most abundant species were *Calanus finmarchicus/glacialis*, *Metridia longa*, *Oncaea borealis*, *Oithona similis* and *Microcalanus pygmaeus*. Between 40 and 80 % of the individuals consisted of *O. borealis*.

The vertical distribution of copepods in relation to water stratification (Arctic surface water, an intermediate layer of Atlantic origin and a deep layer of Arctic water) is discussed. Five species were found in the Atlantic water layer only, while those species occurring in surface and deep layers were also found in the layer of Atlantic origin. Indications of diurnal vertical migrations covering several hundred meters are presented and these results are compared with observations from previous investigations.

INTRODUCTION

A multidisciplinary Swedish Arctic expedition took place during the summer of 1980. The vessel used was a Swedish icebreaker (YMER) which could operate in areas of severe ice conditions. The overall objective of the expedition was to integrate a large number of both biotic and abiotic disciplines in order to gain a better understanding of the Arctic ecosystems. In this perspective, planktology was one of the major disciplines. This paper will deal with the zooplankton material, and the copepods in particular.

The first major investigation on copepods in the Arctic was published by G. O. Sars in 1900. Since then a number of investigations have been carried out, mainly in the Canadian and Russian parts of the Arctic (Brodsky, 1950; Grainger, 1965 and Hughes, 1968). Other work has been carried out during ice-drift expeditions such as "Alpha" (Johnson, 1963), "Arlis II" (Minoda, 1967; Hopkins, 1969 a, 1969 b) and "Fram I" (Andersen, 1984).

Despite all the work of previous investigators, our knowledge of the copepod fauna in the Arctic is still very insufficient, especially with reference to the ecology and vertical distribution of the copepods.

The aim of this study was to make a survey of the vertical distribution of copepods in relation to hydrography in the areas between Svalbard and Frans Josef Land and in the deeper part of the Nansen Basin. In this context, it was of particular interest to study the qualitative effects on the fauna caused by North Atlantic water penetrating into the Polar Basin.

Another aspect of the vertical distribution of copepods at these latitudes, where there is constant daylight during the summer, was the possible occurrence of diurnal migrations. Although this has been mentioned in previous works (Ussing, 1938; Bogorov, 1946 and Digby, 1954), much remains to be studied.

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*Contribution from the YMER-80 expedition

MATERIALS AND METHODS

Investigation area

The area investigated was between Svalbard and Frans Josef Land, approximately between the latitudes 79^{o}N and 82^{o}N and the longitudes 14^{o}E and 45^{o}E (Fig. 1).

Sampling was thus carried out both in the shelf area of the Barents Sea and in the deeper parts of the Nansen Basin.

Sampling

A total of 58 samples was taken at 23 different stations during the period 5 July - 19 August, 1980.

Zooplankton samples were collected by vertical fractionated hauls, normally from 500-250, 250-100 and 100-0 m. In addition, a number of surface hauls were sorted into one haul from 100-20 m and one from 20-0 m. On two occasions, hauls were also made from 2000-1300 and 1000-500 m. The gear used was a UNESCO WP-2 net with a mesh-size of 90 μm. The hauling speed was 0.5-1.0 m x s^{-1}. All samples were preserved in formalin buffered with di-sodium tetraborate, with a formaldehyde concentration of 2 % and a pH between 7 and 8 (UNESCO, 1976).

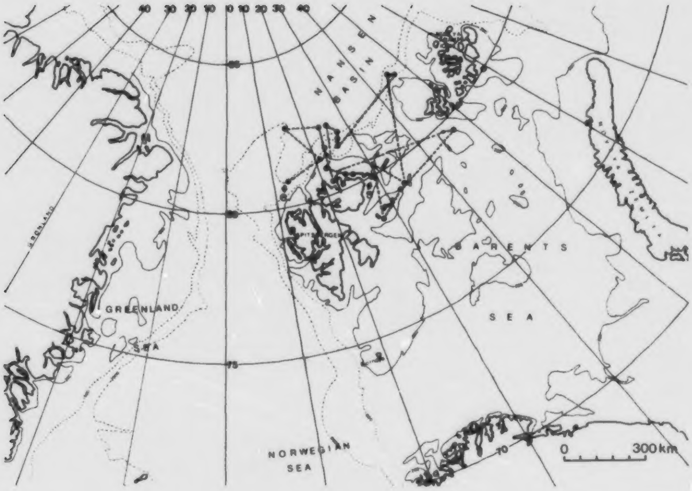
Analysis

The macro-zooplankton (mainly ctenophores, amphipods, euphausids and pteropods) were sorted onboard, while the remaining smaller size fraction was split into subsamples at the laboratory using the system described by Kott (1953). In order to detect less abundant species, the complete sample was always checked along with the subsample.

All organisms in the samples were counted and identified to species. The developmental stages of copepods (excluding the nauplius stages) and the sex of adults were determined. Copepod nauplii were counted but not identified to species. For the analysis, a stereo microscope (Nikon xxx 9-40 x magnification) was used. For the identification of species we mainly referred to Sars (1903) and Rose (1933). The two closely related species Calanus finmarchicus and Calanus glacialis were grouped together due to the difficulties of separating the copepodite stages.

Hydrography

Temperature and salinity were measured with a CTD zond. The results have been placed at our disposal by the Department of Oceanography, University of Goeteborg, Sweden.



40
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NANSEN BASIN
GREENLAND
GREENLAND SEA
SPITSBERGEN
BARENTS
SEA
NORWEGIAN SEA
70
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Figure 1. *Map of the investigation area, including sampling stations (Arrows indicate start and end of the expedition).*

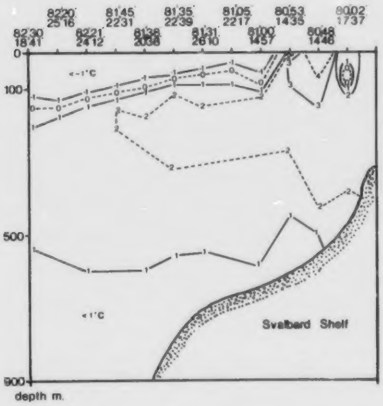

Figure 2. *General description of the isotherms for the investigation area.*

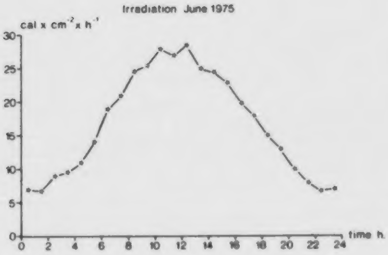

Figure 3. *Irradiation (cal x cm^{-2} x h^{-1}) at Spitsbergen (78^{o}55'N, 11^{o}56'E), June 1975. Diurnal variation calculated from a ten-day period, June 18-28. (After Vinje, 1976).*

RESULTS

Hydrography

Generally speaking, the water column in the Arctic Ocean consists of three layers: Arctic surface water with a temperature of -1.8° C and a salinity of 33.0 o/oo, Arctic deep water with a temperature of -0.6° C and a salinity of 34.9 o/oo, and water originating from the North Atlantic, in an intermediate layer (with a thickness of 600-700 m) with a temperature above 0° C and a salintiy of 34.9 o/oo (Coachman, 1963).

The west Spitsbergen current carries warm Atlantic water into the Polar Basin. The Atlantic water flows eastward along the shelf north of Svalbard and here it may even reach the surface (Aagaard *et al.*, 1981). Figure 2, which illustrates the isotherms in the area north of Svalbard (from 80°02'N to 82°30'N), confirms this general description of the three water layers and the presence of the inflowing Atlantic water.

Ice conditions

The ice conditions varied along the cruise (Palosuo, 1981) South of N 80°, between Svalbard and Frans Josef Land, there was an area with drift-ice. Between N 80° and N 82°, the ice cover increased. This ice had been formed during the previous fall and winter and its thickness reached 1.5 m. North of N 82° we encountered multiyear ice (> 2 m thick) with pack ice formations which reduced our speed considerably.

Irradiation

In order to obtain an approximate value for the irradiance in the area, data from measurements at Spitsbergen in 1975 have been used (Vinje, 1976). Figure 3 illustrates the diurnal variation calculated from a ten-day period, June 18-28, 1975.

Composition of the copepod fauna

Table 1 shows the species encountered during the cruise and their distribution in the water column.

Twenty three species of copepods were identified (18 calanoids, 3 cyclopoids and 2 harpacticoids). The most abundant species were *Oncaea borealis*, *Oithona similis*, *Microcalanus pygmaeus*, *Calanus finmarchicus/glacialis* and *Metridia longa*. Between 40 and 80 % of the individuals consisted of *O. borealis*.

TABLE 1. *Copepod species found during the cruise, and their vertical distribution.*

SPECIES / DEPTH (m)		2000-1300	1000-500	500-250	250-100	100-20	20-0
Augaptilus glacialis (SARS)	a. m.						
	a. f.				x		
	juv.						
Calanus finmarchicus/glacialis	a. m.				x	x	
	a. f.			x	x	x	x
	c. 4-5	x		x	x	x	x
	c. 1-3		x	x	x	x	x
Calanus hyperboreus (KROYER)	a. m.						
	a. f.	x	x	x	x	x	x
	c. 4-5	x		x	x	x	x
	c. 1-3	x			x	x	x
Calanus sp.							x
Chiridius obtusifrons (SARS)	a. m.						
	a. f.	x	x	x	x		
	juv.			x	x		
Gaidius brevispinus (SARS)	a. m.						
	a. f.			x			
	juv.						
Gaidius tenuispinus (SARS)	a. m.			x	x		
	a. f.			x	x		
	juv.		x	x	x		
Heterorhabdus norvegicus (BOECK)	a. m.		x	x	x		
	a. f.		x	x	x	x	
	juv.		x	x	x	x	x
Metridia longa (LUBBOCK)	a. m.		x	x	x	x	x
	a. f.		x	x	x	x	x
	c. 4-5		x	x	x	x	x
	c. 1-3		x	x	x	x	
Microcalanus pygmaeus (SARS)	a. m.			x	x	x	
	a. f.	x	x	x	x	x	x
	juv.	x	x	x	x	x	x
Paraeuchaeta glacialis (HANSEN)	a. m.						
	a. f.			x	x		
	juv.				x		
Paraeuchaeta norvegica (BOECK)	a. m.			x	x	x	
	a. f.			x	x	x	
	juv.				x	x	
Pseudocalanus elongatus (BOECK)	a. m.						
	a. f.			x	x	x	x
	juv.				x	x	x
Pseudocalanus sp.							

Table 1 (continued)

SPECIES / DEPTH (m)		2000-1300	100-500	500-250	250-100	100-20	20-0
Scaphocalanus magnus (T. SCOTT)	a. m.						
	a. f.			x	x	x	
	juv.			x	x	x	
Spinocalanus abyssalis (GIESBRECHT)	a. m.						
	a. f.					x	x
	juv.						
Undinella oblonga (SARS)	a. m.						
	a. f.			x			
Oithona similis (CLAUS)	a. m.				x	x	x
	a. f.	x	x	x	x	x	x
	juv.	x	x	x	x	x	x
Oithona spinirostris (CLAUS)	a. m.				x	x	
	a. f.					x	
	juv.						
Oncaea borealis (SARS)	a. m.	x	x	x	x	x	x
	a. f.	x	x	x	x	x	x
	juv.	x	x	x	x	x	x
Harpacticoid copepod gen. sp.					x	x	x
Microstella sp.					x	x	x
Copepoda gen. sp.		x		x	x	x	x
Copepoda nauplii gen. sp.		x	x	x	x	x	x

Vertical distribution of copepods

Surface layer: Oithona similis and Calanus finmarchicus/glacialis were the most dominant species in the surface layer (100-0 m). On those occasions when the surface hauls were split into 100-20 and 20-0 m layers, the two species were concentrated to the uppermost layer (Fig. 4). The nauplii were not identified to species, but they were with few exceptions always found in the hauls from 20-0 m (Table 1).

Intermediate layer: The intermediate layer of Atlantic origin showed the highest diversity of copepod species. Of the 18 species found from 500-100 m, five were found exclusively in this layer (Augaptilus glacialis, Gaidius brevispinus, Gaidius tenuispinus, Paraeuchaeta glacialis and Undinella oblonga). Chiridius obtusifrons and Scaphocalanus magnus were also most common in this layer. However, the surface and deepwater layers, contained species that were also present in the intermediate layer with only one exception (Spinocalanus abyssalis in the surface layer) (Table 1).

Deepwater layer: The analysis of the two deepwater samples (1000-500 and 2000-1300 m) indicated a gradual reduction in abundance and diversity with depth. The 1000-500 m haul, which sampled both Arctic deep water and water of Atlantic origin, contained 10 species, while the deepest haul contained only 7 species (Table 1).

Diurnal vertical migration of copepods

From the results, it is evident that the investigation area contains both species with clear indications of vertical migration and those that show few or no signs of migration.

In Figure 4, *Oncaea borealis* is chosen as an example of a vertically migrating species and *Oithona similis* illustrates a species with no migrating behaviour.

From Figure 4 it is evident that *Oncaea* appears abundantly all through the water column. However, it is only found in great numbers in the deep hauls (500-250 m) during daytime, while at night the greatest abundances are found in the surface layer. These indications of diurnal vertical migration are more obvious among the adult females than among the juveniles. Signs of similar migrating behaviour were also found in *Microcalanus pygmaeus*. Another plausible migrator is *Metridia longa*. In this species, which has its greatest abundance in the 100-250 m layer during the day, large numbers of animals, exclusively female, were found at the surface during the night.

Quite a different pattern was found in *Oithona similis* (Fig. 4). This species dominated with almost no exception, in the upper layers throughout the whole 24 hour period. Similar non-migrating behaviour was found in *Calanus finmarchicus/glacialis*. However, since no separation of the two species *C. finmarchicus* and *C. glacialis* has been made, it is difficult to interpret the results.

DISCUSSION

A prerequisite for a meaningful comparison of the results of different investigations is a good knowledge of the accuracy of the sampling methods used. The lack of standardized methods and gear, and data on the accuracy of the gear is very conspicuous in previous copepod investigations in the Arctic (Harding, 1967). The use of a net, which is too coarse will sample the smaller species (like *Oithona* and *Oncaea*) and juveniles poorly. On the other hand, nets which are too fine can reduce the filtering capacity and cause clogging (Smith *et al*. 1968). Furthermore, the lack of a closing device on the nets used in previous investigations has reduced the possibilities of a thorough study of the vertical distribution of copepods.

For the reasons mentioned above, the results from earlier investigations can in most cases only be used for a general comparison.

According to our results, *Oncaea borealis*, *Oithona similis*, *Microcalanus pygmaeus*, *Calanus finmarchicus/glacialis* and *Metridia longa* were the dominating species in the area. This is in accordance with results from both the Canadian Basin (Grainger, 1965; Hughes, 1968) and Greenland waters (Minoda, 1967; Andersen, 1984).Of the five dominating species, *O. borealis* was the most abundant. Hughes (1968) and Andersen (1984), who used mesh sizes of 215 and 80µm respectively, came to the same conclusion, while Johnson (1963) and Minoda (1967), who used 330 and 550 um mesh sizes, found few *Oncaea*.

The vertical distribution of copepods in the area is influenced by the water stratification, the amount of food available and the light conditions. As was found by Brodsky (1956) the surface layer contained the greatest abundance of copepods. This is also the zone with the highest concentration of chlorophyll-a (Hernroth and Edler, 1981). The intermediate layer of Atlantic origin had the largest diversity, while the deepest layer was both qualitatively and quantitatively the poorest.

Our results indicate that five species are found in the intermediate layer only (Table 1). Results from Grainger (1965), Harding (1967) and Dunbar and Harding (1968) support these findings for Augaptilus glacialis, Gaidus brevispinus and Undinella oblonga. Dunbar and Harding (1968) state, however, that it is questionable whether any copepod species in the Arctic can be labelled as indicators of a specific water mass. Our findings, that with the exception of one species (Spinocalanus abyssalis), all species that occurred in the surface and deep layers also appeared in the intermediate layer, support their reservation. Furthermore, the occurrence of diurnal vertical migration in the area would presumably increase the vertical zone of distribution for several species and thus lessen the importance of the water stratification.

Figure 3 illustrates that despite the phenomenon of the midnight sun in summer, there is a pronounced diurnal variation in irradiance at these latitudes. Although the sampling program did not focus on studies of diurnal migration, the fact that our sampling was carried out at all hours of the day has enabled us to obtain a general view of the extent of migration.

Of the five dominating copepod species in the area, two (Oncaea borealis, Metridia longa) appear to be migrators, while two (Oithona similis, Calanus finmarchicus/glacialis) show few or no signs of migration (Fig. 4). Although there was no 24-hour sampling at one fixed station, the results indicate that for species like Oncaea and Metridia, migration can cover several hundred metres (Fig. 4) If this is the case, several conclusions can be drawn: 1) The diurnal variation in irradiance during the Polar summer is large enough to produce a pattern of vertical migration similar to that found in more southerly latitudes (Hardy, 1958). 2) To some species and developmental stages, the water stratification does not constitute a barrier. 3) The absence of diurnal migrations by copepods during the Polar summer in some previous investigations (e. g. Bogorov, 1946 and Hughes, 1968) can be attributed to a program which sampled relatively shallow water layers.

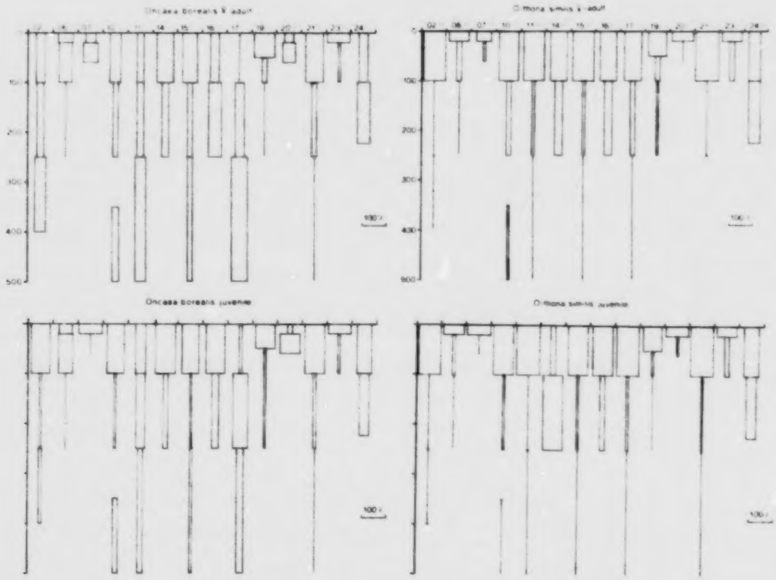

Figure 4. *Diurnal vertical distribution of adult females and juveniles of two common copepods; **a)** a plausible diurnal migrator Oncaea borealis and **b)** a non-diurnal migrator Oithona similis (relative distribution with depth interval).*

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EUDIAPTOMUS GRACILIS (COPEPODA, CALANOIDA): DIEL VERTICAL MIGRATION IN THE FIELD AND DIEL OXYGEN CONSUMPTION RHYTHM IN THE LABORATORY

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Abstract: The diel migratory rhythm of Eudiaptomus gracilis was investigated both in the field and as the diel rhythm of oxygen consumption in the laboratory. The diel migration of Limnocalanus macrurus in the field was also investigated. The animals of Eudiaptomus maintain an increase in oxygen consumption between 24.00 and 03.00 hours. This is in accordance with the field results, which show an ascent of the individuals to the surface layer after midnight.

INTRODUCTION

Diel vertical migration among zooplankton is extensively investigated. A list of recent investigations in the Baltic is given by Gyllenberg (1981). Work has also been done on the endogenous periodic activity rhythms of zooplankton in the lakes of British Columbia (Duval and Geen 1976). They concluded that zooplankton maintain their rhythm in spite of the absence of external stimuli as temperature and light. This short report demonstrates the diel vertical migration of two calanoid copepods, Eudiaptomus gracilis (Sars) and Limnocalanus macrurus Sars as changes of frequency distributions, and for Eudiaptomus as the corresponding changes in respiratory activity in the laboratory.

METHODS

Individuals of Eudiaptomus gracilis and Limnocalanus macrurus were sampled at lake Pääjärvi (southern Finland) (Gyllenberg 1981). The samples were taken with a Sormunen sampler (length 1 m, volume 6.4 l) as vertical series from the bottom to the surface, filtered through a 25-µm net and preserved with formalin. One sample was taken at each depth. For Eudiaptomus 100-500 individuals were caught at each sampling date, and for Limnocalanus 10-20 individuals were sampled. The samples were left to settle in 50 ml cuvettes for some hours. An inverted microscope was used for counting. The central point of the frequency distribution column was calculated as

$$\sum_{s=1}^{n} (D_s \times N_s) / N$$

where D_s = mean depth of sample s, N_s = number of specimens in sample s and N = Total number of specimens, n = number of samples in a column.

Living Eudiaptomus individuals were introduced into a respiration chamber (1 ml) and the oxygen consumption was measured with a polarographic equipment according to Gyllenberg and Lundqvist (1976). Some 20 animals were used in the chamber during each experiment (experimental period 12 hours) at 20°C with 3 hours light, 6 hours dark and 3 hours light condition (normal daylight). In all 6 experiments were performed, on which the curve in Fig. 2 is based.

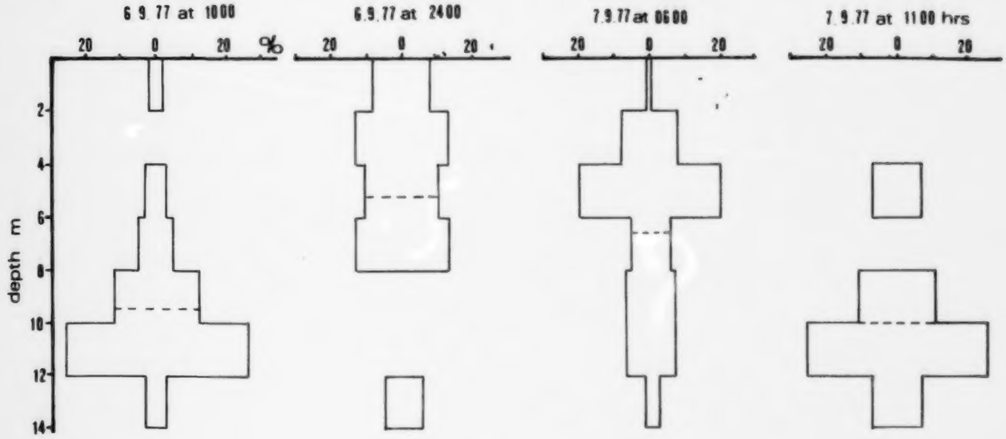

Figure 1A. *Distribution of Eudiaptomus gracilis numbers in the different layers of lake Pääjärvi in 1977, given as percentages of the total numbers, ---- central point of distribution.*

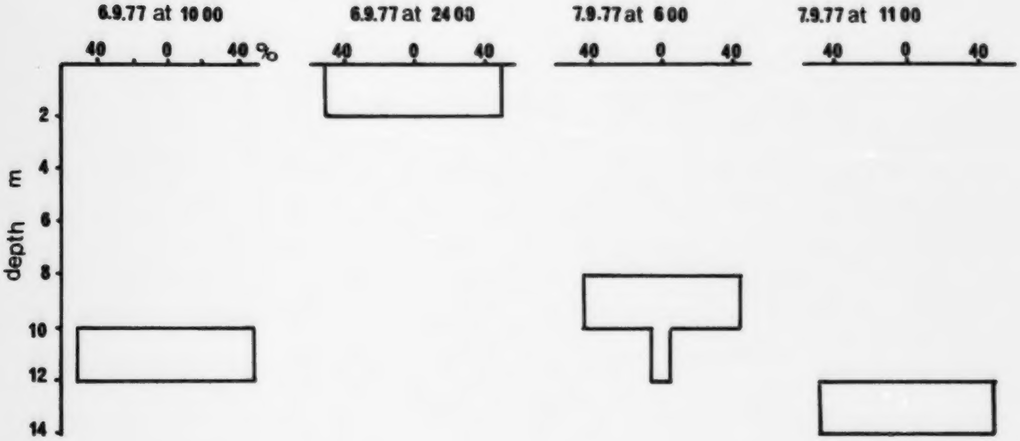

Figure 1C. *Distribution of Limnocalanus macrurus numbers in the different layers of lake Pääjärvi, given as percentages of the total numbers, 10-20 individuals were sampled on each sampling date.*

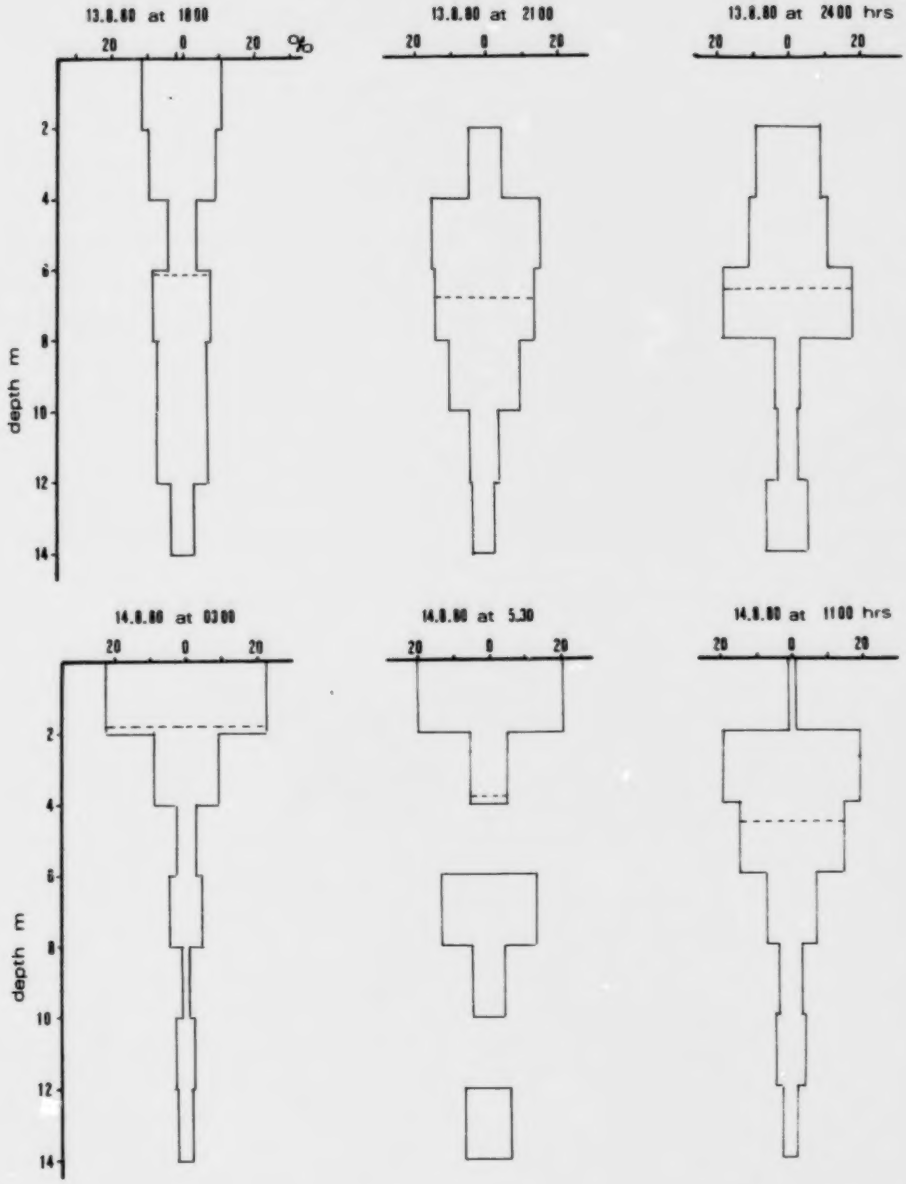

Figure 1B. *Distribution of* *Eudiaptomus* *gracilis* *numbers in the different layers of lake Pääjärvi in 1980, given as percentages of the total numbers, ---- central point of distribution.*

RESULTS

Fig. 1 shows that both Eudiaptomus gracilis and Limnocalanus macrurus migrate to the surface during the night (when it is dark), and sink back to deeper layers during daytime. Since the dark period started earlier in 1977 (Fig. 1 A and 1 C) the light conditions evidently act as a trigger initiating migration to the surface, which occurred earlier in 1977 than in 1980. The weather conditions on both sampling dates were clear cloudless sky. The ascent of Limnocalanus is still more distinct than that of Eudiaptomus and it seeks cold water again immediately after the grazing period at about 24.00 hours.

Fig. 2 shows how respiratory activity is adjusted to the diel periodicity rhythm on 14.8.1980. It appears that ascent is done in two peak stages: at first there is a larger peak at about 24.00 and then a smaller peak at 03.00 hours. The activity then gradually decreases until the resting metabolic rate is achieved at about 07.00 hours. The peak at 24.00 hours is significantly different from the preceding level ($P < 0.01^{**}$), whereas the 03.00 peak is not statistically different ($P > 0.1$). The activity period evidently starts at 24.00 hours and it takes three hours for the animals to reach the surface (Fig. 1 B).

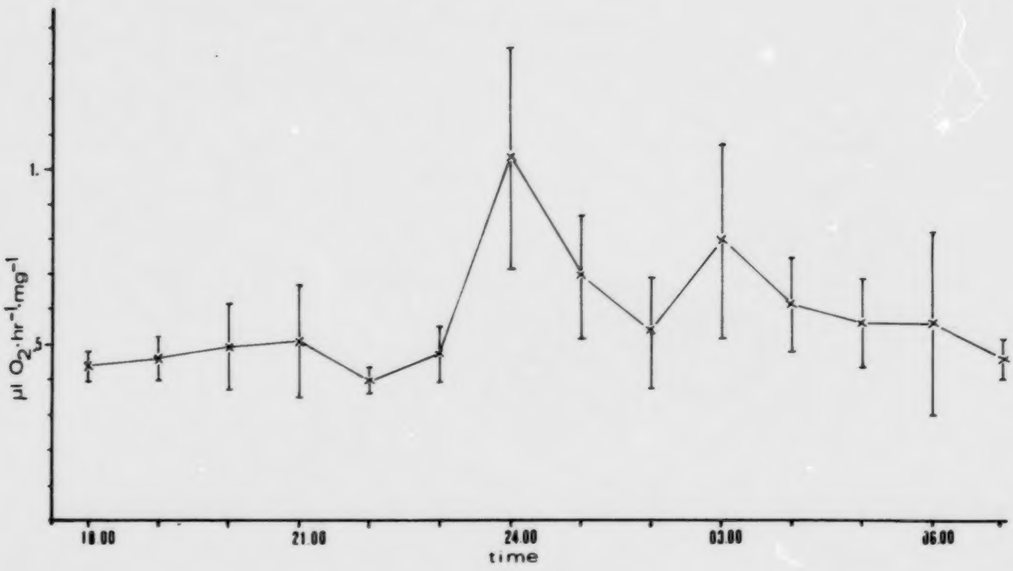

Figure 2. *Diel oxygen rhythm in Eudiaptomus gracilis as affected by daylight in the laboratory The value at 24.00 hours is significantly different from the preceding level ($P < 0.01^{**}$). The experiment was carried out simultaneously with the field experiment on August 14, 1980.*

DISCUSSION

These results are not consistent with those found by Duval and Geen (1976). They investigated diel rhythms in zooplankton at a constant temperature and absence of periodic light stimuli. Their results showed a bimodal activity rhythm with peaks at 06.00 and 18.00 hours with low activity in between. The present peaks are at 24.00 and 03.00 hours during the ascent period. The results presented are also in accordance with the peak in numbers observed at 03.00 hours in the field. It appears that the typical midnight sinking period and respiratory activity again in the early morning hours is more or less absent in Eudiaptomus.

A typical bimodal vertical migration rhythm with midnight sinking period is also demonstrated for Daphnia magna (Cladocera). It appears that an activity peak during midnight is also present in Limnocalanus macrurus. In this case the movement during different times of the day is very distinct. Apparently Limnocalanus start to rise to the surface before midnight. Limnocalanus is known as a stenothermal (oligothermal) species and therefore it seeks out deeper and colder layers of the lake except for a short feeding period at midnight. Unfortunately the material is based on only 10-20 individuals caught at each sampling date.

The ascent to upper layers during night represents also a relocation of energy resources. The animals that stay in the upper layers are preferably feeding fresh phytoplankton that has been assimilating during the day. Not only is there a relocation of energy sources but also an energy discharge to respiratory losses during the ascent. This energy discharge must be compensated by extensive feeding during the midnight period.

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OBSERVATIONS ON XARIFIID COPEPODS PARASITIC IN SCLERACTINIA

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Abstract: The poecilostomatoid family Xarifiidae contains four genera: Xarifia, O rstomella, Lipochrus, and Zazaranus, with Xarifia being by far the largest with 75 species. Xarifiids have been found only in shallow-water Scleractinia, and the incidence appears to be related to the distribution of the corals. Host preferences are seen in species of Xarifia where 17 occur only in various species of Acropora and 41 live only in single coral species. The geographical distribution of xarifiids ranges from the Red Sea and Madagascar to Japan-Enewetak Atoll-New Caledonia. These copepods are absent in the eastern Pacific (Hawaii, Panama, Moorea). Xarifiids occur in each of the five suborders of the Scleractinia, but mostly in the Astrocoeniina. Several groups of apparently related species of Xarifia have been identified and confirmed by the construction of a dendrogram.

The family Xarifiidae is a well-defined group. The body is elongate and transformed, usually less than 3 mm in length, with weakly defined segmentation. The region dorsal to the fifth legs in the female of many species bears processes or knobs. The mandible is a small simple blade or absent. Legs 1-4 have 2- or 3-segmented exopods; the endopods are 1- or 2-segmented, rudimentary, or absent. Leg 5 has a free segment bearing 1 or 2 setae, is reduced to 2 or 3 setae, or is entirely absent.

The four genera in the Xarifiidae (Xarifia Humes, 1960, Orstomella Humes and Ho, 1968, Lipochrus Humes and Dojiri, 1982, and Zazaranus Humes and Dojiri, 1983) are distinguished mainly by the segmentation of the legs and the presence or absence of processes above the fifth legs in female.

Xarifia, the largest of the four genera with 75 species, is known only from shallow-water hermatypic corals, where it lives in the polyps. The geographical distribution of Xarifia is limited by the ecological requirements of the corals. Corals grow best from 25° to 29°C (Wells, 1956). Species of Xarifia have been found in the Red Sea-Madagascar area eastward to an arc formed through Japan-Enewetak Atoll-New Caledonia in 93 species of corals. Xarifia is absent as far as known from the Pacific Ocean east of 166°; corals examined in Hawaii, Moorea, and Panama contained no Xarifia.

Xarifiidae are not present in corals in the Caribbean. In pre-Pliocene times xarifiid coppepods perhaps had not evolved or had not spread from the presumed origin in the Indo-Malayan region eastward toward the then still open straits between the Caribbean and the eastern Pacific Ocean. The increasingly continental coastal environment in the Tertiary and the disappearance of many coral genera from the Panamanian region by the end of the Oligocene, plus the effect of the East Pacific barrier, may have prevented xarifiids from moving eastward. Although a few species of several Indo-Pacific coral genera, such as Acropora, Favia, Porites, and Tubastrea, are living today in the Caribbean, they are not parasitized by xarifiids but by another family of highly transformed poecilostomatoid copepods, the Corallovexiidae, described by Stock (1975).

Obviously current information on the distribution of Xarifia depends on the thoroughness and efficiency with which the coral species in a given region have been examined. Two hundred and eleven collections have been made over a wide area. The most intensive collecting has been done in Madagascar (45 collections), the Moluccas (50), New Caledonia (68), and on the Great Barrier Reef in

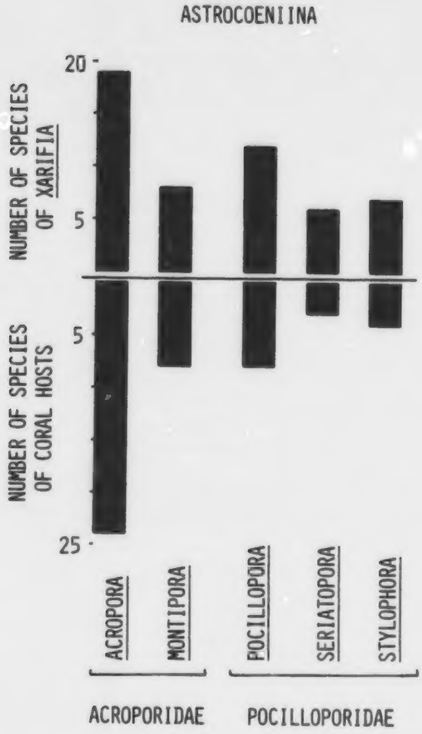

Figure 1. *Number of species of* *Xarifia* *(above central line) and number of species of coral hosts (below central line) in genera of Astrocoeniina.*

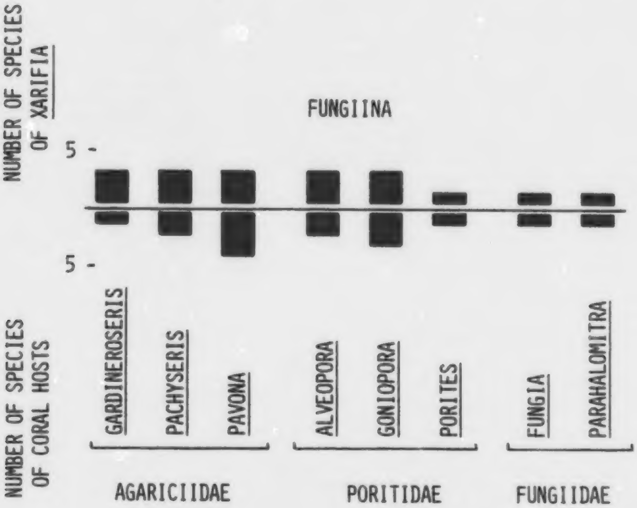

Figure 2. *Number of species of* *Xarifia* *(above central line) and number of species of corals hosts (below central line) in genera of Fungiina.*

Australia (26). Only a few collections have been made in the Red Sea, Mauritius, the Maledives, Japan, and at the Enewetak Atoll. Concentrated effort for a very short time in a region rich in corals may result in the collection of many xarifiids. For example, during field work of only three hours at Karang Mie, a small reef on the eastern coast of Halmahera, in the Moluccas, 15 species of *Xarifia*, 9 of them new, were collecteed from 8 species of corals hosts.

Recovery of these copepods from the coral polyps depends on the method of collection. Few xarifiids will be found in washings of corals soon after collection. Freshly collected corals should be isolated in approximately 5 % solution of ethanol in sea water for several hours, then shaken and rinsed thoroughly. The wash water is strained through a fine net, with about 120 holes per 2.5 cm. In this way it is possible to recover several hundred *Xarifia* from one small coral colony.

Determination of infestation rates is often difficult, since corals are colonial hosts often of such large size that it is often not possible to examine the entire colony.

For studies of host specificity in *Xarifia* the host corals must be identified with certainty. The identification of Scleractinia is difficult in some cases because of the existence of growth forms and intraspecific variation. In the genus *Pocillopora*, for example, more than 40 species have been named, but 10 to 15 of these are probably not valid species (Wells, 1972).

Host specificity of *Xarifia* exists at the generic level. Nearly half of the 75 species of *Xarifia* are known from only one species of coral. For these *Xarifia* host specificity at the species level is undeterminable, since collections are very limited in number. At the genus level, however, host specificity can be observed. For example, 17 species of *Xarifia* occur only in various species of *Acropora*. Sometimes one xarifiid species will spread over several host species, for example, *Xarifia breviramea* in 9 species of *Acropora*. On the other hand, the number of species of *Xarifia* living in a single coral species may be large, for example, 9 species of *Xarifia* in *Acropora hyacinthus*. As many as 7 species of *Xarifia* have been recovered from a single colony of *Acropora florida* in New Caledonia. Sixty-seven species of *Xarifia* (88%) occur in only one genus of coral. However, five records of *Xarifia* may be considered to be from accidental hosts. If these are discounted, the number of species of *Xarifia* parasitizing one host genus rises to 72 or 96 %

Xarifia occurs in all five suborders of Scleractinia (Table 1). The Astrocoeniina, including the protean family Acroporidae (with about 200 species) and the Pocilloporidae, have the greatest number of xarifiid parasites (Fig. 1); the Fungiina (Fig. 2), the Faviina (Fig. 3), the Caryophylliina (Fig. 3), and the Dendrophylliina (Fig. 3) have much smaller numbers of parasites.

Table 1. *Occurrence of Xarifia in five suborders of Scleractinia*

	Number of species of corals	**Number of species of *Xarifia***
Astrocoeniina	47	35
Fungiina	15	18
Faviina	13	10
Caryophylliina	4	4
Dendrophylliina	3	3

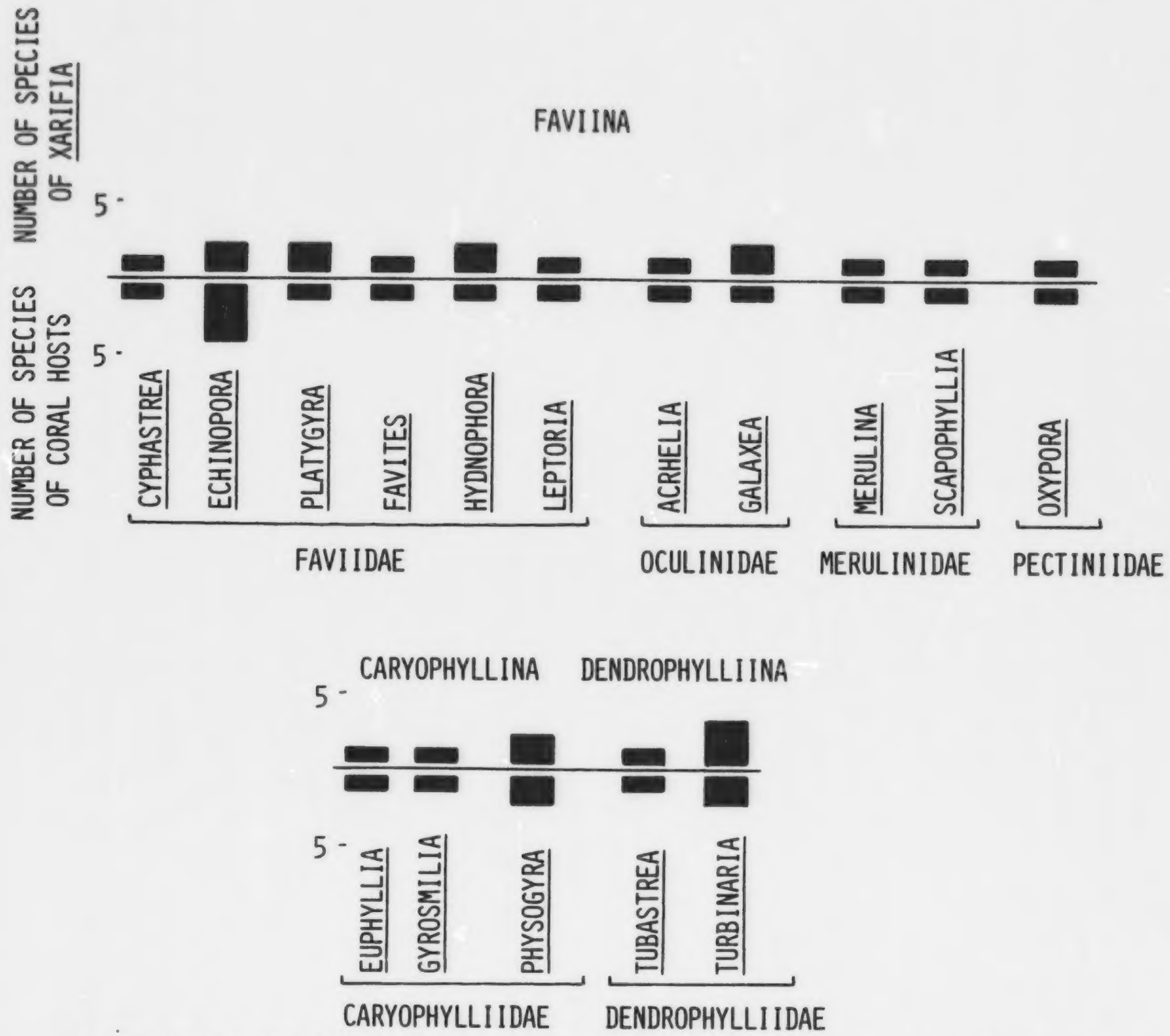

Figure 3. *Number of species of Xarifia (above central line) and number of species of coral hosts (below central line) in genera of Faviina, Caryophylliina, and Dendrophylliina.*

Evolution within the Xarifiidae is difficult to determine. Although there is no fossil record of these copepods, certain coral hosts such as *Goniopora* and *Hydnophora* date from the Middle Cretaceous, about 100,000,000 years ago. Many other genera such as *Acropora*, *Montipora*, *Pocillopora*, and *Porites* appeared in the Eocene 50,000,000 years later. Still other genera such as *Acrhelia*, *Merulina*, and *Physogyra* are known only from Recent times. Roots of the Astrocoeniina and Fungiina extend to the Middle Triassic (Wells, 1956). Given the highly transformed nature of the Xarifiidae, presumably acquired only after a very long period of evolution, it is tempting to think that the ancestors of present day xarifiids may have lived in the Middle Triassic astrocoeniine and fungiine corals. Perhaps they may have had an antecedent history as associates of rugose corals, a group that became extinct in the Permian.

Whatever the origin of the Xarifiidae, the ancestral form probably had a combination of plesiomorphic features seen in living *Xarifia*. The region dorsal to the fifth legs in the female was smooth, rather than with processes or knobs. The eggs were arranged in cluster, rather than being seriate. The second antenna was 4-segmented, rather than 3-segmented. Legs 1-4 had 3-segmented exopods and 2-segmented endopods, rather than 1-segmented endopods. Leg 5 in the female had a free segment, rather than being reduced to 3 setae or entirely absent. The caudal ramus was clearly separated from the anal segment, rather than fused with this segment. We can imagine a primitive ancestral form combining such characters.

From such an ancestor a dichotomy may have given rise (Fig. 4) on the one hand to forms that retained a 3-segmented exopod on leg 1, which in turn gave rise later by reduction to forms with the endopods of legs 1-4 being 1- or 2-segmented (*Xarifia*) and those with the endopod of legs 1-4 being rudimentary or absent (*Lipochrus*), and on the other hand to forms with a 2-segmented exopod in leg 1, which gave rise to those with mandibles present (*Zazaranus*) and those without mandibles (*Orstomella*).

Among present day *Xarifia* we can see examples of relationships in triplets or pairs of relationships, based on shared external morphological features and host preference. An example is to be found among the three species *X. decorata* Humes and Ho, 1968, *X. fissilis* Humes, in press, and *X. jugalis* Humes, 1985, all living in corals belonging to the family Pocilloporidae, and all showing several features in common. They have a similar body form. There are three long processes above the fifth legs in the female. The eggs are arranged serially. The second antenna is 4-segmented with a long terminal claw. The exopod of leg 1 has an outer spine on each segment but in the exopods of legs 2-4 the spine on the second segment is replaced by a seta. The 2-segmented endopods in legs 1-4 have the setal formula 2, 2, 1, 1, except *X. decorata* with 3, 3, 1, 1. Leg 5 in the female has an elongate free segment. In a dendrogram constructed from a cluster analysis using 26 character states for all 75 species, the slight difference in setal formula for the endopods of legs 1 and 2 is reflected in the grouping of the three species (Fig. 5). Other examples of relationships observed morphologically and confirmed by cluster analysis are *X. diminuta* Humes and Ho, 1967, and *X. lamellispinosa* Humes and Ho, 1968, *X. obesa* Humes and Ho, 1968, and *X. varilabrata* Humes, in press, and *X. extensa* Humes and Dojiri. 1982, and *X. temnura* Humes and Ho, 1968.

Much more remians to be learned about these parasites of corals. Nothing is known about the development of Xarifiidae. The way in which the copepods are spread from one coral colony to another is unknown. The effect of the copepods on the corals is also unknown, except for one brief observation of the copepods tearing the coral tissue with their spines (Gerlach, in Humes, 1960). Taxonomically, xarifiids as a group are incompletely known. Sixteen species have been collected in such small numbers (one or two specimens) that descriptions have not been attempted. Less than one-fourth of the species

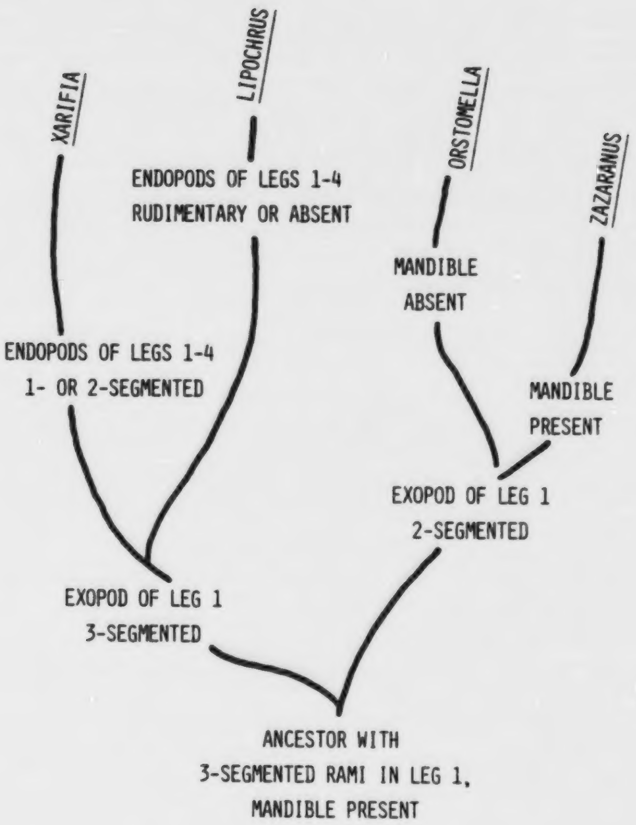
XARIFIA
LIPOCHRUS
ORSTOMELLA
ZAZARANUS
ENDOPODS OF LEGS 1-4 RUDIMENTARY OR ABSENT
ENDOPODS OF LEGS 1-4 1- OR 2-SEGMENTED
MANDIBLE ABSENT
MANDIBLE PRESENT
EXOPOD OF LEG 1 2-SEGMENTED
EXOPOD OF LEG 1 3-SEGMENTED
ANCESTOR WITH 3-SEGMENTED RAMI IN LEG 1, MANDIBLE PRESENT

Figure 4. *Phylogeny of the four genera of the Xarifiidae.*

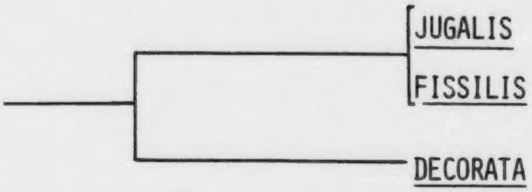
JUGALIS
FISSILIS
DECORATA

Figure 5. *Relationships of Xarifia jugalis, X. fissilis, and X. decorata as expressed in a dendrogram based on a cluster analysis using 26 character states organized for 75 congeners.*

of living reef-building Scleractinia have been examined for these parasites. It is not known whether xarifiid copepods parasitize nonreef-building or ahermatypic corals. Many unanswered questions concerning the Xarifiidae remain.

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STUDIES ON THE PRODUCTION OF PLANKTONIC COPEPODS FOR AQUACULTURE

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Abstract: Mass culture of the cyclopoid copepod *Apocyclops borneoensis* Lindberg, was carried out in 15 m^3 capacity outdoor culture tanks. Under experimental conditions, the harvest averaged 2.75×10^6 copepods d^{-1} with a maximum of 4.4×10^6 copepods m^{-3}. Experiments conducted on the salinity tolerance of this species show that a salinity of 20‰ is optimum for mass culture. Using copepods for aquaculture is discussed.

INTRODUCTION

Copepods constitute an important feed component in the marine food chain and are in great demand for aquaculture. The copepod species selected for aquaculture should have optimum production under controlled conditions, a rapid life cycle, high reproductive potential and good resistance to adverse culture conditions, e.g., space limitations, lack of food and accumulation of metabolic products, that could possibly interfere with production rate. Precise knowledge of adequate conditions of exploitation is also required to guarantee a steady yield.

Liao et al. (1971) opined that the quality, size, density and mobility of the food are important factors for developing larval rearing techniques. In hatcheries, copepods are used only to a limited extent because they are not readily available. Natural sources, i.e., collected plankton, are expensive and unreliable due to quantitative and qualitative fluctuations and to the danger of introducing harmful organisms (parasites and predators). Also, cultivation of calanoids, the most prevalent planktonic copepods, has not reached a sufficiently large scale. Brackish water cyclopids have recently been introduced in mariculture (James and Thirunavukkarasu, 1980).

This investigation deals with the mass culture and production of the planktonic cylopoid copepod *Apocyclops borneoensis* Lindberg, in 15 m^3 capacity out-door culture tanks with a working volume of 10 m^3. Feeding copepods to the larvae of the marine fish *Acanthopagrus cuvieri* was also investigated. The salinity tolerance and production dynamics of *A. borneoensis* are discussed.

METHODS

The cyclopoid *Apocyclops borneoensis* was isolated from plankton collections made in the saline lagoons (salinity 12-15‰) near Penang Airport in Malaysia. Seven pairs of *A. borneoensis* were brought to Kuwait and scaled up using 200 *ml*, 500 *ml* and 1 *l* capacity beakers for preliminary observations. The marine yeast *Candida* sp. (Al-Hinty and James, 1983), at a rate of 20 mg $l^{-1}d^{-1}$, was initially used to feed the copepods.

The salinity tolerance of *A. borneoensis* was studied in 5*l* capacity beakers placed in a water bath with a temperature controller maintaining the water at 28°C. This temperature was based on preliminary observations showing that a temperature of 27-30°C is most conducive for rearing A. borneoensis. The salinity tolerance experiment was carried out using 0, 10, 20, 30, and 40‰ water salinities in four replicates. The initial stocking density average 500 copepods l^{-1}. Baker's yeast was used at a rate of 10-20 mg $l^{-1}d^{-1}$ for feeding the copepods during the period of observation. The water was continuously aerated at a rate of 100 ml air min^{-1}. Copepods were sampled each four days to estimate survival. Final copepod counts were made after two weeks of observation.

The duration of development of A. borneoensis was determined by maintaining culture of gravid females in test tubes in a multi-block heater with interchangeable tube blocks (Tecom Dri block model 0B3) to maintain the temperature at 28°C. The copepods were fed baker's yeast. The time between hatching of the egg and development of copepodite I was considered the duration for naupliar development and the duration between copepodite I and the development of copepodite VI (i.e, adult) was taken as the life span of the copepodite stage.

Copepods were produced experimentally in a 15 m^3 capacity (3 m x 3 m x 1.65 m) concrete tank provided with a heating system to maintain water temperature at 28°C. The tank was aerated by 12 mm diameter PVC pipes perforated with holes of 1 mm diameter at 50 cm intervals. The aeration pipes were fixed at the bottom of the tank by stainless steel masonry fasteners. The tank had a central sump with a 75 mm diameter PVC drain value.

From the beaker cultures, the copepods were scaled up in 30 l and 500 l capacity tanks. The 500 l capacity tank cultures were used to initiate the copepod culture in the 15 m^3 capacity tanks. Water salinity was maintained at 20-25‰, by adding seawater diluted with fresh water. The culture was gradually increased to 10 m^3 on the 11th day of the observation period by frequent addition of diluted seawater (ambient seawater salinity, 40‰). The copepods were fed with baker's yeast at a rate of 20 mg $l^{-1}d^{-1}$. In addition, Chlorella sp. isolated from local seawater were added at a rate of 0.6 g $m^{-3}d^{-1}$ to maintain water quality. The water was continuously aerated at a rate of 100-150 ml air min^{-1}. Aliquot samples of 1 l culture were taken twice weekly. Counts were made of the adults, copepodites and nauplii. Along with each sampling, measurements of salinity, dissolved oxygen and pH were obtained.

Two sets of experiments were conducted on feeding A. borneoensis or Artemia nauplii to the larvae of Acanthopagrus cuvieri. In the first experiment, 13 day old sobaity (A. cuvieri) larvae were stocked at a rate of 2 larvae l^{-1} in 100 l capacity tanks. They were fed three types of feed in four replicates. The feed consisted of Artemia nauplii alone, Artemia nauplii mixed with copepods (50% each) and copepods alone. The feeding rate was 1 prey organism $l^{-1}d^{-1}$ on the first two days and 2 prey organisms $l^{-1}d^{-1}$ from the third day onwards. The experiment tanks were placed in a water bath to control the water temperature. Aliquot samples were obtained once each 24h to maintain the prey concentration. The experiment was terminated when the fish larvae were 21 days old. The length and weight were measured after anaesthetising the larvae with MS 22.

In the second experiment 21 day old sobaity larvae were stocked in 30 l capacity panlites placed in a water bath to control the water temperature. The initial stocking density was 2 larvae l^{-1}. They were fed same three types of feed in the three replicates. The feeding rate was 2 prey organisms $l^{-1}d^{-1}$. The experiment was terminated when the fish larvae were 31 days old. The final length and weight were measured after anaesthetising the larvae with MS 22.

RESULTS

Studies on the salinity tolerance of A. borneoensis show that the species is euryhaline (Fig. 1). But the polynomial regression shows that an optimum salinity of about 20‰ is most conducive for their mass culture. A sharp decline of copepods occurred when the water was not saline.

During this investigation the observed duration of development at 28°C and 20‰ was three days from nauplii to copepodite I and four days for copepodite I to copepodite IV.

Table 1. *Production of Apocyclops borneoensis in a 15 m^3 capacity outdoor culture tank with a working volume of 10 m^3*

Date	**Days**	**Nauplii** No. l^{-1}	**Copepodites** No. l^{-1}	**Copepods** No. l^{-1}	**Total** No. l^{-1}
18.1.84	1	15	65	58	138
22.1.84	4	30	122	211	363
25.1.84	7	72	176	189	437
29.1.84	11	343	221	96	660
1.2.84	14	295	317	158	770
5.2.84	17	19	204	168	391
9.2.84	21	15	185	177	377
12.2.84	24	9	142	151	302 *
15.2.84	27	7	120	138	265
20.2.84	32	11	103	153	267
26.2.84	38	180	195	262	637
4.3.84	46	1800	1400	1200	4400 **
8.3.84	50	440	296	750	1486
10.3.84	52	600	400	2300	3300 +
14.3.84.	56	215	281	630	1126
18.3.84	60	100	200	800	1100
22.3.84	64	101	109	614	824
25.3.84	67	50	125	375	550

* 604 x 10^3 copepods harvested.

** 22 x 10^6 copepods harvested.

+ 16.5 x 10^6 copepods harvested.

++ 5.5 x 10 copepods harvested.

Table 1 shows the observed production of A. borneoensis during the January to March 1984 culture period. The population increased from 138 individuals l^{-1} to 770 individuals l^{-1} on the 14th day of the observation period. However, a decline in population occurred from 17th day of the observation period. On 24th day of the observation period partial replacement of the culture medium was carried out by removing 2 m^3 (604 x 10^3 copepods) of the culture and replacing it with fresh culture medium. Then onwards the population recovered and reached a maximum density of 4400 individuals l^{-1} on the 46th

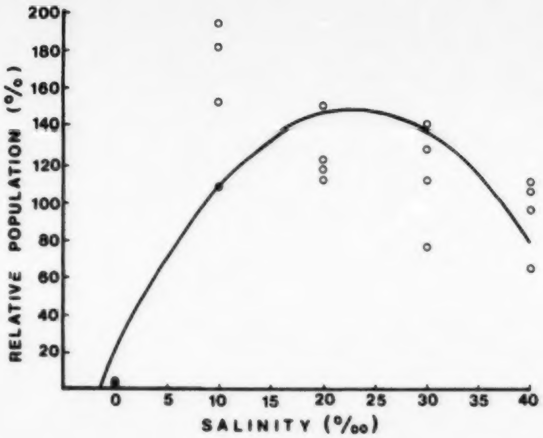

Figure 1: *Salinity tolerance of A. borneoensis.* $y = a + bx + cx^2$, *i.e., relative population*
$= 21.86 + 11.02738 \times \text{Salinity} - 0.023946 \times (\text{sal})^2$;
$n = 20$, $r^2 = 0.6115011$.

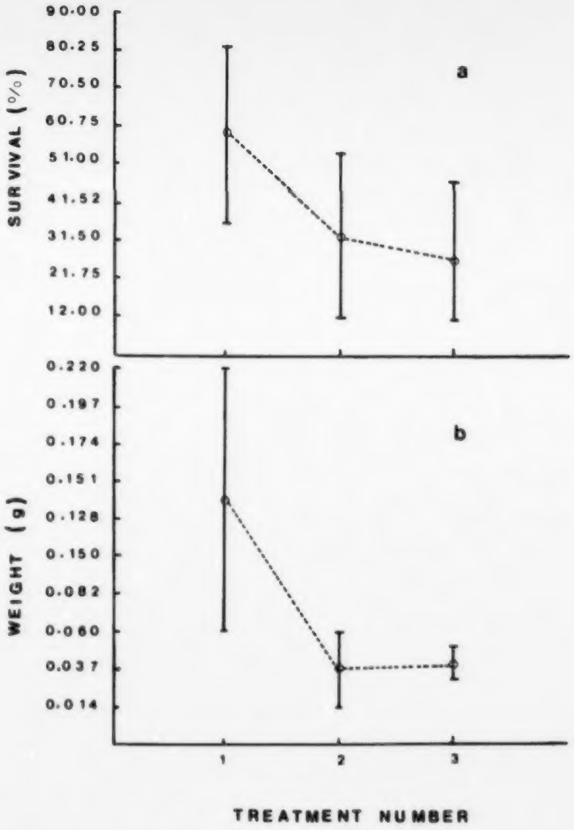

Figure 2: *Multiple comparison plot-LSD using Artemia (Treatment No. 1), Artemia and copepods (Treatment No. 2) and copepods (Treatment No. 3) for 13-21 day old fish larvae: (a) Survival; (b) Total weight.*

day of the observation period. From 46 to 60 days of the observation period, the harvest averaged 2.75×10^6 copepods d^{-1} with a maximum of 4.4×10^6 copepods m^{-3}.

Although temperature was controlled by a heating system, temperature fluctuations of 1.6°C (from 27.7 to 29.3°C) were observed. The water salinity was maintained at 20-21‰. The pH varied between 7.02 and 7.31 and DO between 4.0 and 4.6 mg l^{-1}. The fluctuation in the *A. borneoensis* population is not due to lack of food. As it was a closed culture system, adequate amounts of feed were regularly supplied. The feed quality and maintenance of the culture system should be investigated further.

Experiments conducted on the use of *A. borneoensis* or *Artemia* nauplii for feeding 13-21 day old sobaity larvae show (Fig. 2) that feeding with *Artemia* nauplii gives a significantly increased survival of up to 83% ($P \leq 0.05$) compared with feeding copepods alone. Feeding *A. borneoensis* and *Artemia* nauplii to 21-31 day old sobaity larvae shows (Table 3) that copepods mixed with *Artemia* nauplii give significantly increased survival of up to 96% ($P \leq 0.05$) and biomass 1.098g ($P \leq 0.05$) compared with *Artemia* nauplii alone. Also the use of copepods alone give better survival (up to 76%) compared to the use of *Artemia* nauplii (survival up to 64%) alone.

Table 2. *Use of copepods (M. dengizicus) and Artemia nauplii for feeding 13 to 21 day old larvae of Acanthopagrus cuvieri*

Treatment	Replicate	Survival (%)	Mean sd	Length (mm)		Average weigth per larva (g)	Total weight (g)	Mean ± sd
				Range	Mean ± sd			
Artemia nauplii	1	62	56.5 ±18.06	6.00 - 8.67	7.74 ± 0.98	0.0019	0.167	0.137 ±0.061
	2	46		6.67 - 8.00	7.07 ± 0.53	0.0009	0.059	
	3	83		5.33 - 8.67	7.55 ± 1.33	0.0019	0.220	
	4	35		6.67 -11.73	9.20 ± 1.96	0.0021	0.103	
Artemia nauplii + Copepods	1	12	24.73 ±17.16	6.00 - 8.67	7.20 ± 1.22	0.0009	0.014	0.033 ±0.017
	2	20		4.67 - 8.00	5.92 ± 1.27	0.0008	0.022	
	3	54		5.33 - 8.67	6.93 ± 1.23	0.0008	0.060	
	4	13		6.00 - 9.07	7.68 ± 1.00	0.0019	0.034	
Copepods	1*	-	-	-	-	-	-	-
	2	46	24.33 ±15.36	5.33 - 9.47	6.47 ± 1.38	0.0008	0.051	0.032 ±0.014
	3	15		4.67 - 9.87	6.93 ± 1.70	0.0008	0.016	
	4	12		6.00 - 9.07	7.55 ± 0.99	0.0019	0.030	

* Deleted due to mass mortality at the start of the experiment

Table 3. *Use of copepods (M. dengizicus) and Artemia nauplii for feeding 21 to 31 day old larvae of Acanthopagrus cuvieri*

Treatment	Replicate	Survival (%)	Mean ± sd	Length (mm)		Mean weight per larva (g)	Total weight (g)	Mean ± sd
				Range	Mean ± sd			
Artemia nauplii	1	64	62.67 ±0.94	10.67-17.33	13.90 ± 1.65	0.0222	0.710	0.728 ± 0.013
	2	62		11.33-16.67	14.11 ± 1.20	0.0239	0.741	
	3	62		10.67-16.00	13.90 ± 1.31	0.0236	0.732	
Artemia nauplii + copepods	1	72	84 ±9.80	10.67-17.33	14.01 ± 1.95	0.0293	1.055	1.098 ± 0.152
	2	84		10.67-17.33	13.57 ± 1.74	0.0223	0.937	
	3	96		11.33-16.00	13.70 ± 1.04	0.0271	1.301	
copepods	1	68	72 ±3.27	10.67-18.67	13.48 ± 1.95	0.0267	0.935	0.861 ± 0.106
	2	76		10.67-16.00	12.61 ± 1.59	0.0187	0.711	
	3	72		10.67-18.67	13.85 ± 1.91	0.0260	0.936	

DISCUSSION

Lindberg (1954) described this species obtained from tidal marshes in Borneo. The species in Malaysia is restricted to saline habitats. The salinity tolerance of this species has not been investigated so far. The results obtained during this investigation shows that this species could be adapted and reared in salinities of 30-40‰, although it does better at lower salinities. This species could very well tolerate the ambient salinity of sea water in Kuwait (40‰) making them useful for aquaculture in this area.

The short duration of development (seven days) observed could enhance the production rate. However, this depends on temperature and diet as discussed by Taube and Nauwerck (1967), Burgis (1970) and Smyly (1970). While discussing the effect of diet and temperature on the development of *Mesocyclops leuckarti* (Claus), Jamieson (1980) observed that diet would affect the fecundity of copepods. Further investigations are necessary to understand the effect of different diets and temperature on the duration of development of *A. borneoensis*.

Although the use of copepods for feeding 13-21 day old larvae did not yield significant improvement when compared with the use of *Artemia* nauplii, the results obtained on the use of copepods for feeding 21-31 day old *A. cuvieri* larvae show that either copepods alone or copepods mixed with *Artemia* nauplii at a ratio of 1:1 could yield better survival and growth than the use of *Artemia* nauplii alone.

Lebour (1919a, b) reported copepods as the most common food of nearly all very young fishes and Blaxter (1965) concurred. Atlantic herring (*Clupea harengus*) larvae reared in the laboratory selected copepod nauplii and copepodites as food (Rosenthal, 1969). Blaxter (1969) implied that copepod nauplii were the food of laboratory-reared pilchard (*Sardina pilchardus*) larvae, based upon an examination of the composition of wild plankton offered as food and from the analyses of stomach contents of larvae collected at sea. Detwyler and Houde (1970) confirmed the utility of copepod nauplii and copepodites as food for both anchovy Anchoa mitchilli and scaled sardine Harengula pensacolae larvae. The results of this investigation agree, and show that as fish larvae grow, they prefer large size food organisms such as copepods instead of small ones like Artemia nauplii.

Although zooplankton is considered to be the most preferred food of the fry of the most fin fishes, some zooplankton are reported to be predaceous on fish fry. Several authors have reported the attack of fish fry by cyclopoid copepods (Oliva and Sladecek, 1950; Fryer, 1953; Davis, 1959; Fabian, 1960; Lakshmanan, 1969; Slevaraj and Rao, 1977). No such incidents occurred in this study. This investigation shows that cyclopoid copepods could partially or completely replace expensive Artemia nauplii in aquaculture.

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FACTORS AFFECTING THE ELIMINATION OF TROPODIAPTOMUS SPECTABILIS AND ITS REPLACEMENT BY METADIAPTOMUS TRANSVAALENSIS IN AN OLIGOTROPHIC LAKE

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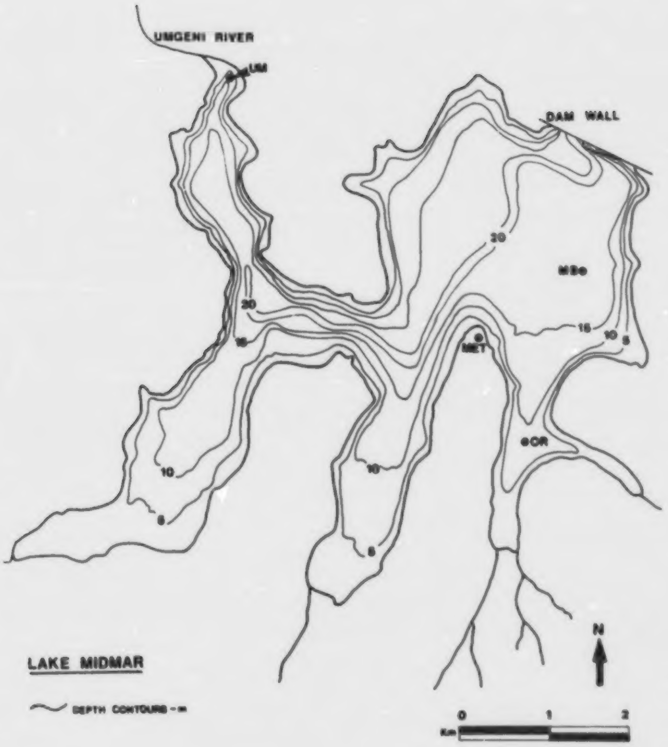
Abstract: During the latter half of 1981, Tropodiaptomus spectabilis, the only calanoid in Lake Midmar, a warm-temperate oligotrophic lake in the Natal midlands of South Africa was replaced completely by Metadiaptomus transvaalensis, a similar species of comparable size. The pH of the lake is usually neutral but early in 1981 there was a rise in pH (sometimes to above 9) and it seems probable that this favoured M. transvaalensis which has been recorded as a species of alkaline waters. The appearance of M. transvaalensis in March 1981 coincided with the infestation of T. spectabilis by an ellobiopsid parasite, an organism to which M. transvaalensis was essentially immune. The parasite is a new species of ellobiopsid and is the first record of this taxonomically-uncertain group from freshwater. By the end of 1981, M. transvaalensis not only replaced T. spectabilis completely but produced higher numbers than had been recorded for T. spectabilis in earlier sampling programmes.

There is little doubt that these two species are in competition with each other. M. transvaalensis has a clutch-size which is about five times that of T. spectabilis and also an egg-development time which is comparably shorter especially at low temperatures. T. spectabilis is said to be a warm-water species and in 1981, water temperatures in winter were 1°C lower than usual. While these factors must have had an effect, the main reduction in competitive ability came from the parasite load. The cusp catastrophe model of Thom may be applied to conceptualise the behaviour of the two different calanoid populations, using the control variables of pH and competitive ability. A severe drought during 1983 when lake levels fell to below 20% introduced other ecological factors and it was only in May, 1984 after the impoundment had returned to full supply, that T. spectabilis again established itself as the only calanoid species in Lake Midmar.

INTRODUCTION

Tropodiaptomus spectabilis (Kiefer, 1929) was found by Hutchinson et al. (1932) to be present in four seasonally astatic and two perennially astatic pans in Transvaal, South Africa. He recorded Metadiaptomus transvaalensis Methuen, 1910 from alkaline dystrophic waters in the same area. Hutchinson (1967) stated that the latter species is characteristic of turbid water with little or no high vegetation. T. spectabilis was collected by Rayner (1981) from Lake Midmar over a two-year sampling programme from March, 1977 to June, 1979. It was recorded monthly from all four sampling stations over the whole period, although never in high numbers (maximum 6800 m^{-3} in surface waters). On one occasion, June 1979, two breeding females of M. transvaalensis were collected from highly turbid water ($Z_{SD} < 0.5$m) with a pH of 8.85.

After a lapse of 18 months, sampling of Lake Midmar recommenced at the beginning of 1981. It was hoped that a more reliable estimate of the calanoid population in particular, would be obtained by reducing the sampling interval from monthly to weekly. With T. spectabilis as the only resident calanoid, it was felt that an ideal opportunity existed for an in depth assessment of its population structure and seasonal fluctuations. During this two-year sampling period (1981-1982) an unusual sequence of ecological factors occurred, resulting in the obtaining of data on not one but two species of calanoids and the discovery of an ellobiopsid parasite, as yet unrecorded from freshwater, on one of the species (King, 1984).


UMGENI RIVER
UM
DAM WALL
20
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10
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N
LAKE MIDMAR
DEPTH CONTOURS - m
0
1
2
Km

Figure 1. *Bathymetric map of Lake Midmar showing sampling stations. UM = Mgeni; MB = Main Basin; OR = Orient; MET = Meteorological Station.*

THE STUDY AREA

Lake Midmar is a warm-temperature oligotrophic impoundment situated at the altitude of 1044 m in the Natal midlands in the Republic of South Africa, geographical location 29°30'S; 30°12'E. The lake is at maximum capacity (177.2×10^6 m^3) during the summer months when rainfall in the upper catchment usually maintains an assured water inflow. The lake has a dendritic shape (Figure 1) with a central basin and four arms. At full supply the surface area is 15.59 km^2, the maximum depth 22.3 m and the mean depth 11.4 m. The main source of nutrients and allochthonous material is the Mgeni River, a 257 km perennial river which, in providing water for Lake Midmar, drains a catchment of 928 km^2 (Archibald et al., 1979).

Lake Midmar is monomictic with a period of weak stratification during summer and isothermal conditions in winter. Surface water temperatures range from approximately 11 °C in mid-winter to 25°C in summer. An oxygen deficit develops in the hypolimnion during summer but this is largely restricted to the main basin. For an oligotrophic lake, Midmar is highly turbid with Secchi disk readings frequently less than one meter (Walmsley, 1976; Twinch and Breen, 1978a and b; Archibald et al., 1979). The alkalinity (0.33 to 0.66 meq l^{-1}) and pH (around 7) of Midmar are characteristic of a poorly buffered system (Walmsley, 1976; Twinch, 1976). Water entering the lake is low in nutrients (Furness, 1974) resulting in low algal growth potential (Toerien et al., 1975). There is a high diversity of zooplankton species with low standing crops (Rayner, 1981).

METHODS

Zooplankton samples were collected weekly from three sampling stations (Figure 1) using a standard plankton net for vertical hauls and a Clarke-Bumpus sampler for trawls (mesh aperture 62 μm in each case). Temperature, dissolved oxygen, turbidity and pH were measured concurrently while meteorological data were recorded continuously by a small weather station on the lake shore. Plankters were preserved in 4% formalin and analysed according to standard laboratory procedure (Schwoerbel, 1970; Edmondson, 1971; Bottrell et al., 1976).

RESULTS

a. Calanoid populations

From 1977 to 1979, it was known that T. spectabilis was the only calanoid species in the lake, the two female M. transvaalensis recorded being considered to be of little consequence (Rayner, 1981). However, early in the current programme M. transvaalensis was recorded, two adults being collected on 10 March, 1981, one individual carrying eggs; on 30 March, 1981 another female with eggs was recorded. These specimens were found only at Mgeni sampling station, while the first record from Orient was 2 June, 1981 by which stage a breeding population was present at Mgeni. The first M. transvaalensis caught at Main Basin was a female with an egg-scar on 16 June, 1981. All these appearances were preceeded by high pH (Figure 2).

To describe calanoid population structure, percentage graphs were used. These even-out violent fluctuations in total numbers and enable the succession of stages to be followed when numbers are low

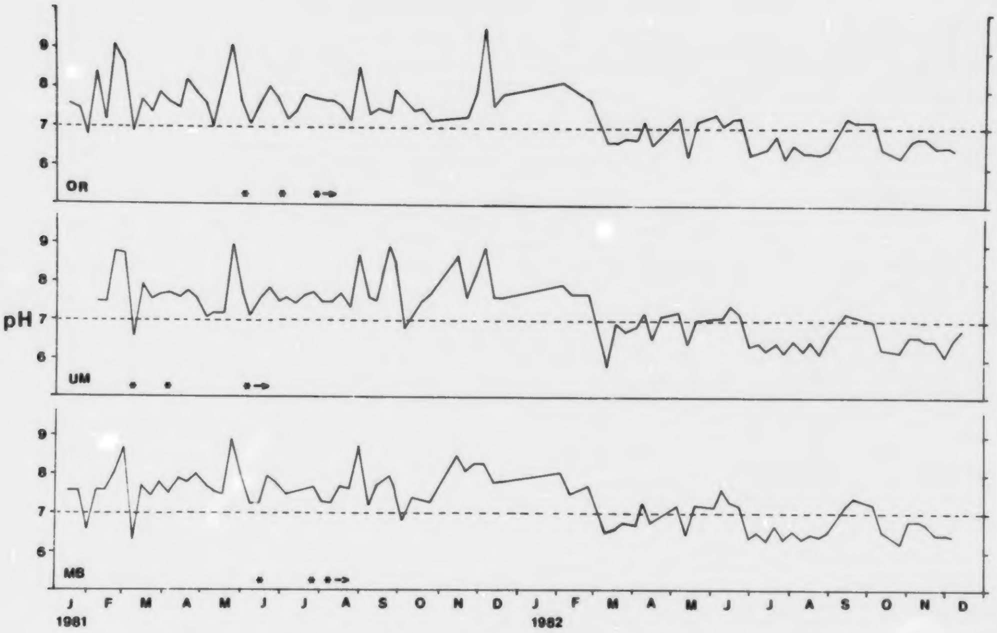

Figure 2. *Surface pH values. Asterisks show the appearance and arrows show the continuous existence of Metadiaptomus transvaalensis at each sampling station.*

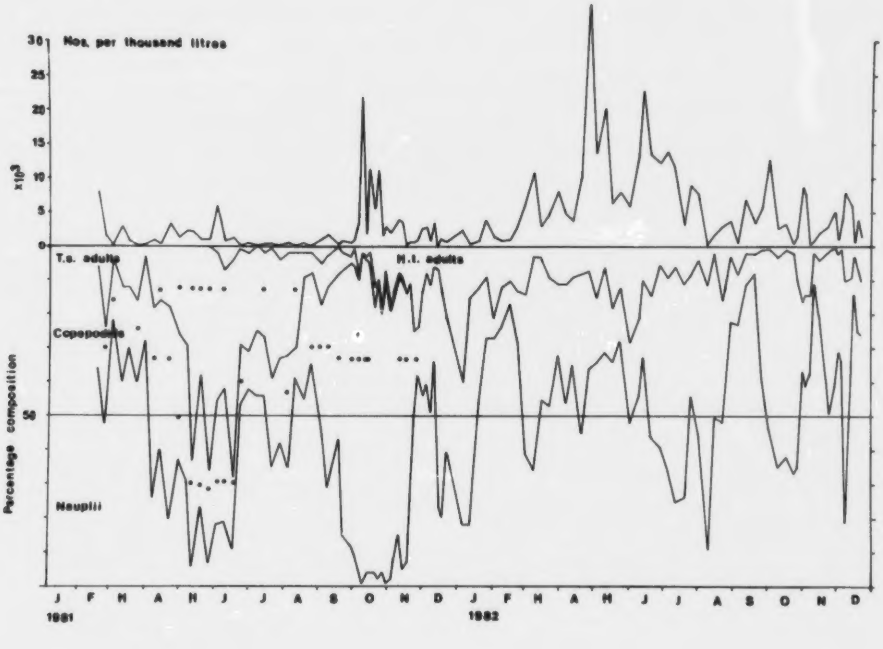

Figure 3. *Calanoida abundance at Mgeni sampling station. A = total calanoid numbers; B = percentage composition of population numbers. T. s. = Tropodiaptomus spectabilis; M. t. = Metadiaptomus transvaalensis. The two species were distinguishable only as adults. Asterisks represent occurrence of parasitised individuals in the sample.*

(Marshall and Orr, 1972). The percentage composition of calanoids from one of the sampling stations, Mgeni, is illustrated in Figure 3. CV copepodid stages were included in the copepodite total. The presence of parasitised individuals is denoted by an asterisk. The diagram (Figure 3) shows clearly how T. spectabilis adults decreased in numbers at a time when M. transvaalensis began to increase and by November 1981 there was a complete species replacement. M. transvaalensis continued to increase in numbers until April and May 1982 when numbers were higher than those recorded for T. spectabilis a year earlier. More than 6000 copepodites m^{-3} were collected from the surface two meters at Mgeni on more than one occasion during April, a figure approaching Rayner's (1981) highest total calanoid count.

b. Parasitism

T. spectabilis was infested with a parasite (Figure 4 A, B, C) similar to Ellobiopsis chattoni as described by Chatton (1920) and Jepps (1937) for Calanus finmarchicus. Although Jepps (1937) was inclined to favour placing the ellobiopsid in the fungi, recent studies give greater credence to regarding them as dinoflagellates (Galt and Whistler, 1970). Despite the uncertainty of its taxonomic status, there is no doubt that the parasite on T. spectabilis is an ellobiopsid and that this is the first record of such a parasite from freshwater (Boshma, 1949, Vader, 1973).

The first T. spectabilis to be infested were recorded from Mgeni station on 23 February, 1981 and 2 March, 1981 when 25% of CV copepodites were affected. During April, 1981, there was a predominance of copepodites with large number parasitised. Records of parasitism on T. spectabilis were similar for all three sampling stations from February - March 1981 until the complete disappearance of T. spectabilis in November, 1981. On two occasions in Orient (18 and 22 September, 1981) M. transvaalensis egg-scarred females were parasitised and in Main Basin on 29 September, 1981 four infested males were collected. Considering the large number of adults present, these data reflect the low susceptibility of M. transvaalensis to the ellobiopsis. It could be said to be essentially immune.

Existing information relating to the presence of T. spectabilis and M. transvaalensis in Lake Midmar 1981-84 is summarised in Tabel 1. As there is an ongoing Midmar Research programme, additional data from continuing research projects have been included (Meyer, 1983; Robson pers. comm.).

DISCUSSION

Hutchinson et al. (1932) described M. transvaalensis as a species of alkaline waters and it could be assumed with some certainty that the elevated pH in Lake Midmar was responsible for the appearance of this calanoid. However, the pH range of this species is 6.8 to 9.2 and that of T. spectabilis 6.8 to 9.1 (Hutchinson et al., 1932). This hardly seems a criterion for separation of these species but the rising pH may have given the initial impetus to M. transvaalensis. Whether the ellobiopsid parasite was also favoured by the higher pH would be difficult to ascertain but the possibility cannot be dismissed. Another ecological factor which may have placed additional stress on the warm-water T. spectabilis, was a winter water temperature of $1^{\circ}C$ lower than normal. This situation continued into the summer of 1981/2 when water temperatures did not reach expected maxima.

M. transvaalensis and T. spectabilis are very similar in size and morphology so presumably are in competition with each other (Hutchinson, 1967). The competitive ability of T. spectabilis seems to have been severely undermined by the ellobiopsid parasite to the point where it was displaced completely by M. transvaalensis. The cusp catastrophe model of Rene Thom (1972) as illustrated by Zeeman (1976) may be used to conceptualise the behaviour of the two different calanoid populations, using the control

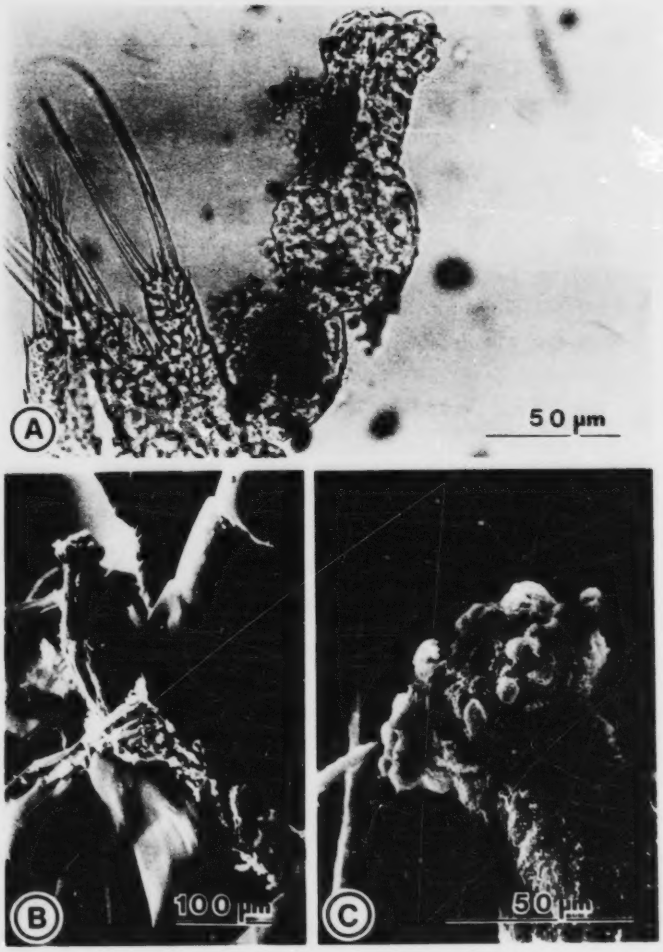

Figure 4. *Ellobiopsid parasite on Tropodiaptomus spectabilis. A = light microscope photograph of the parasite attached to urosome of a stage I copepodite. B = scanning electron micrograph of the parasite attached to a male at articulation of cephalosome and metasome. C = detail of "gonomere".*

Table 1. *Summary of existing information relating to the presence of T. spectabilis and M. transvaalensis in Lake Midmar, 1981 -1984.*

Months	1981	1982	1983	1984
January				
February	*T. spectabilis* dominant	lower summer water temperatures than usual		Lake level rose from 50% Jan. to 90% March lake full 16.04.1984
March	Appearance *M. transvaalensis* first appearance of parasite		Lake level continued to drop and by April was 10% of full supply	
April		pH normal		
May				Three *M. transvaalensis* collected in May, 84 and thereafter only *T. spectabilis* (Robson, pers. comm.)
June	*M. transvaalensis* well-established at river station appearance at others		*M. transvaalensis* was present from March through August (Meyer, 1983)	
July				
August	During 1981 raised pH, lower temperatures than usual	lake level began dropping from August (73%) and by December fell to 45%	Lake level June, July, August. 19%	
September				
October				
November	complete replacement of *T. spectabilis* by *M. transvaalensis*		Lake level November 19% rose in December	
December				

variables of pH and competitive ability. With constantly high competitive ability, changing pH, population numbers will fluctuate slightly, as they will with constantly low pH and fluctuating competitive ability. But when the two control variables change at the same time catastrophic population behaviour may result. In this case lowered competitive ability of *T. spectabilis* due to the parasite load, plus raised pH favouring *M. transvaalensis* lead to a catastrophic population crash in *T. spectabilis*. During 1982 the pH dropped to below 7, but by this time *M. transvaalensis* had completely replaced *T. spectabilis* so its competitive ability remained high. This result is predicted by the model, as the two species have reversed their positions on the behaviour surface and with fluctuating pH, the numbers of both species will fluctuate only slightly as they did at the beginning of 1981. Egg development times of *M. transvaalensis* are also comparably shorter than those of *T. spectabilis* at low temperatures (G. Robson, pers. comm.). Adding temperature as a third control variable would give a more complex (swallow tail) catastrophe model, but this would not alter the outcome of population changes. The competitive ability of *M. transvaalensis* would have been further enhanced by its much higher clutch size (50-60) when compared with a mean of 11.9 for *T. spectabilis* (Rayner, 1981).

At a time when lake conditions might have returned to "normal", lake levels began to drop because of severe drought and by December 1982 the lake was 45% full. These conditions continued into 1983 when the lake was only 10% full in April and remained under 20% for the whole year. Unfortunately no physico-chemical data were collected over this period. Good rains eased the drought and the lake filled again by April 1984. By May 1984, only a few *M. transvaalensis* remained and by June, *T. spectabilis* regained its 1977-79 rôle of the only calanoid species in the lake. No parasitised individuals have been recorded since the recovery.

ACKNOWLEDGEMENTS

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TIME ADAPTATION OF THE NUTRITIONAL PROCESSES OF NERITIC COPEPODS

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Abstract: Digestive enzymes are the functional link between ingestion and assimilation. They have been shown to be representative of the nutritional adaptability to the changes in quantity and quality of the food supply. More recent published data suggested that different patterns of time are involved in the processes of regulation by both internal and external factors. From the review of the current literature and unpublished data a more complex physiological model of regulation emerge to explain the variability in copepod digestive enzyme levels. Short term changes (diel type), when noticeable, appear to be independant of the food supply contrary to the medium term ones. Long term acclimation seems directly related to the specific needs. All these sources of regulation are, to some extent, acting in sequence and their implication for the experimenter are discussed.

INTRODUCTION

In a naturally variable trophic environment, the success of the growth and/or the reproductive strategies of a zooplankton population will greatly rely on the ability of the individuals to adapt to such changes. According to Mayzaud and Poulet (1978), such acclimation supposes that the organisms exposed to more food show increase ingestion and digestive enzyme activities and, therefore, enhanced feeding capacity. They mentioned that such response would not be discernable if the stimulus (food change) is too small or occurs over too short a period of time. The experimental results obtained by Cox (1981), Hirche (1981), Cox and Willason (1981), Head and Conover (1983) have confirmed that acclimation required at least 24 to 48 hrs and that for a given stage of growth the level of enzyme activity was positively related to food supply, so long as the trophic environment remains limiting.

The different patterns of enzyme changes observed by Tande and Slagstad (1982) for stage V and adult females of Calanus finmarchicus, captured in the same environment, strongly suggest that growth requirements could also be part of the nutritional regulation processes. Indeed, growth rate is directly related to the fulfillement of the metabolic needs and is associated with an appropriate food supply (Conover, 1978). Digestive enzymes correspond to the functional link between ingestion and assimilation and it seems likely that their acitivities are controlled or related to both food intake and metabolic needs.

If we consider the different time frames relevant to the nutritional history of a copepod, three stages can be defined. Short term events which occurr during the diel cycles of feeding, medium term changes which relate to the natural periodicities of changes of the particulate matter (few days to weeks) and long term events which encompass those events which affect the entire life cycle of the species considered. To what extent the variability in enzyme rates is related to the superimposition of different sets of regulation associated with these different time frames should be clarified to understand the processes which control the adaptative strategy of neritic zooplankton.

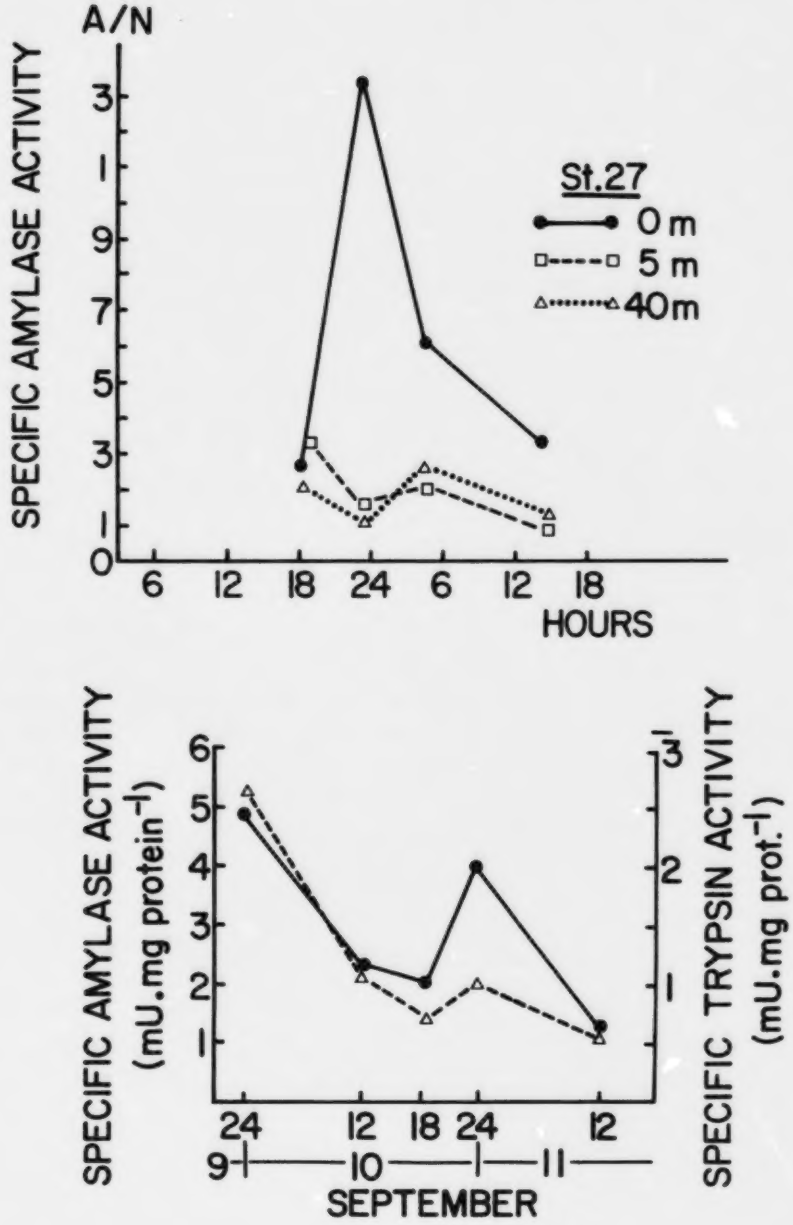

Figure 1. *Diurnal changes in amylase and trypsin activities from a mixed population of copepods (top graph) and from Calanus finmarchicus (bottom graph). Redrawn from Boucher and Samain (1974) and Tande and Slagstad (1982).*

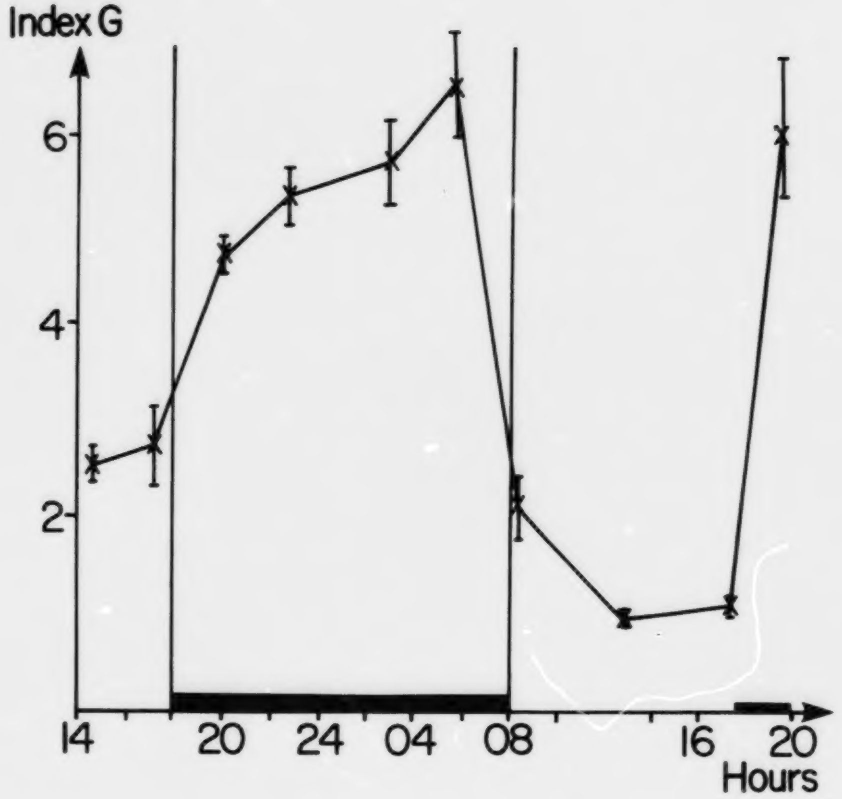

Figure 2. *Circadian rhythm of the gut fluorescence index (G) of Clausocalanus arcuicornis stage V and females. Redrawn from Mayzaud et al. (1984).*

Short term-diel type changes

Since the introduction of gut fluorescence measurements, circadian periodicity in phytoplankton ingestion has been demonstrated in a growing number of zooplankton species (Mackas and Bohrer, 1976; Grossnickle, 1979; Dagg and Grill, 1980; Baars and Oosterhuis, 1984; Mayzaud et al., 1984). Such periodicity may occurr in all herbivorous species of copepods inhabiting the same environment (Mackas and Bohrer, 1976), or one or two of several (Head et al., 1984).

The demonstration of a rhythmicity in digestive enzyme activities is more controversial. Most studies have been carried out on vertically migrating species with the basic assumption that since they are spending their dark hours feeding in the chlorophyll rich surface layer, their level of enzyme should be related to the food supply. Diel rhythms were reported by Boucher and Samain (1974) for mixed populations copepods and by Tande and Slagstad (1982) for stage V, Calanus finmarchicus. In both studies they found that either amylase or trypsin showed maximum and minimum acitivities respectively around midnight and midday or in the afternoon (Fig. 1). Other results by Boucher and Samain (1975) and Boucher et al. (1976) failed to show similar well-marked rhythmicity but presented some evidence that the magnitude of the day-night enzyme variability was probably inversely related to the natural trophic situation. To ascertain a diel rhythmicity of the nutritional metabolism, measuring the changes in digestive enzyme rate is necessary but not sufficient. Indeed, as indicated by Baars and Oosterhuis (1984) such changes must be in phase with those of the ingestion rate since diel feeding periodicity may be found without related enzyme changes and vice-versa.

Recent data reported by Mayzaud et al. (1984), showed some evidences of diel changes in both feeding rate and digestive enzyme activities for a population of mediterranean zooplankton dominated by the copepods Clausocalanus and Paracalanus. Gut pigment content measurements were carried out on stage V and female Clausocalanus, and varied from day time low levels of 1 to 3 to night time maxima of 4 to 7 (Fig. 2). Digestive enzymes were analyzed on the total zooplankton population. Activities of different carbohydrases were influenced by day-night successions in varying degrees (Fig. 3). Laminarinase increased during the day displayed two night maxima (2016 and 0610) whereas amylase activity decreased during the day time and showed only one sharp, late night maximum (0610). The activities of α and β glucosidases exhibited profiles of variation similar to amylase, while cellulase and β-galactosidase displayed a much reduced periodicity. Acidic proteases showed a totally different pattern of variation (Fig. 4), oscillating over most of the first night, then decreasing sharply just before dawn (0610). Trypsin-like activity showed no specific periodicity over the 30 hrs considered (Fig. 4).

The apparent discrepancy in the published results could probably be resolved by a more realistic interpretation of the relationships between ingestion and digestion. When a clear ingestion rhythmicity is present, digestion must proceed with about the same periodicity, but measurements of digestive enzyme activities do not differenciate between enzyme synthesis and enzyme secretion. Presumably only secretion would reflect the instantaneous digestive activity. Ulstrastructure of the mid-gut of various copepods (Arnaud et al., 1978; 1980) suggests that three cell types (F, R and B) are responsible for most of the digestive processes. Each of these cellular structures undergoes a cycle in which degenerating cells are replaced by newly synthesized ones. If the periodicity of such a cycle is also regulated by the feeding frequency or if the amount of enzyme stored at any time is small compared to the amount secreted, a clear diel rhythmycity should be observed. On the other hand, if new cells and new enzymes are synthesized during digestion at a rate equivalent to the enzyme secretion or if the pool of stored enzyme is large compared to the amount secreted, no rhythm in enzyme activity will be

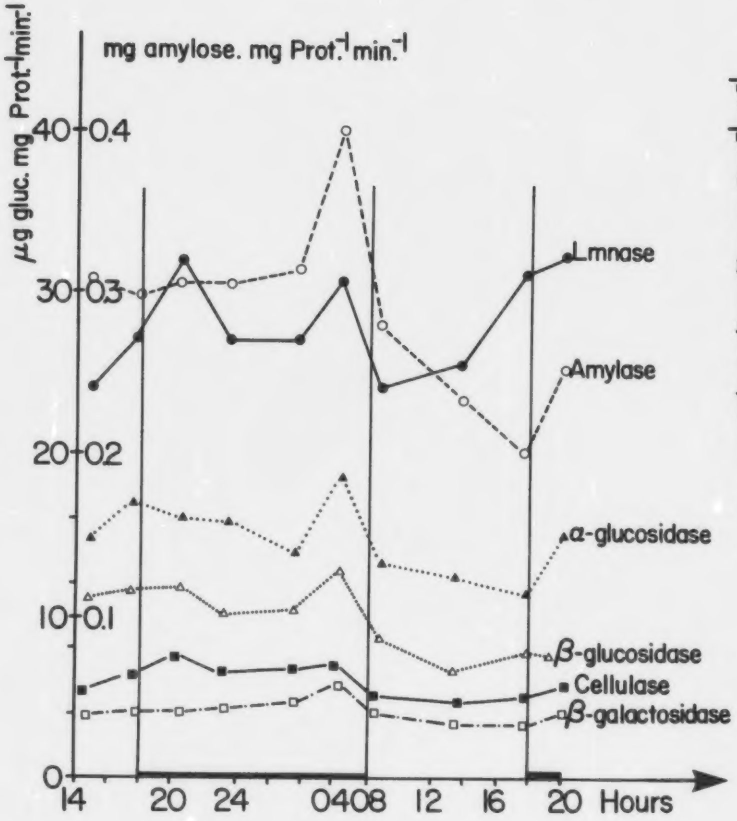

Figure 3. *Diel changes in the carbohydrase acitvities of a total population of zooplankton dominated by C. arcuicornis. Redrawn from Mayzaud et al. (1984).*

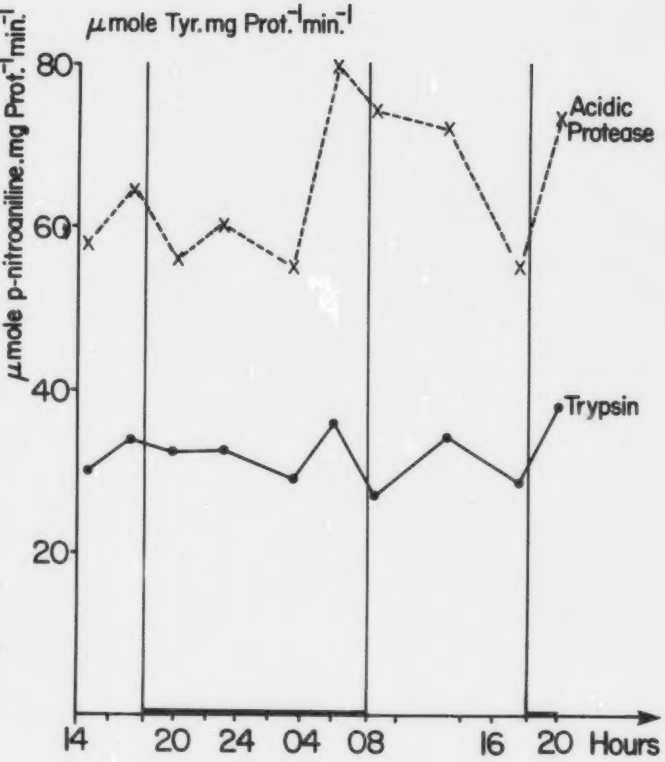

Figure 4. *Diel changes in the protease activities of a total population of zooplankton dominated by C. arcuicornis. Redrawn from Mayzaud et al. (1984).*

observed. To what extent the occurrence of each of such metabolic situation is related to the environmental trophic state deserves further research but seems quite likely.

Medium term regulation of the nutritional processes.

Many laboratory experiments have illustrated the functional response of seston-feeding copepods to increasing concentration of food (Frost, 1980). It is usually described as proportional to food supply up to a certain level, above which it becomes constant. Such maximum ingestion rate has been described as a function of the species considered and the cell size of the phytoplankton offered (Frost, 1974). The results obtained by Poulet (1974) on the seasonal variations of the grazing activity of female copepod *Pseudocalanus minutus* on naturally occurring particles were the first indication that feeding rate was probably not following a saturation type model. Further works by Poulet (1977; 1978), Mayzaud and Poulet (1978), Conover and Huntley (1980); Huntley (1981), Conover and Mayzaud (1984) on different copepod species and growth stages confirmed the idea that over seasons, feeding rate is directly related to food supply and reinforced the hypothesis that, even in coastal waters, the natural trophic state may be: food-limitation.

The seasonal changes in digestive enzyme rate of either total copepod population or given stages of single species of herbivorous copepods described by Mayzaud and Conover (1976), Hirche (1981), Cox (1981), Tande and Slagstad (1982) strongly suggest that food supply also control the rate of digestion. Under stable quality of food, small neritic copepods digestive enzyme activities appeared to be directly related to the changes in food offered (Mayzaud and Conover, 1976), even though each enzyme considered does not relate over time with the same chemical or size descriptor. This last observation suggests that such descriptors do not really correspond to a measure of the enzymatic substrate but merely describe the various aspects of the organic matter present in the diet. The fact that these indexes varied with certain of the enzyme considered are indicative of changes in the nature of the food eaten by the copepods. Similar results were found for large calanoid copepods such as *Calanus finmarchicus*, although most of the significant changes are taking place during the spring bloom of phytoplankton rather than over the rest of the year (Hirche, 1981; Tande and Slagstad, 1982). Indeed overwintering stage IV or V, present during most of summer, fall and winter always displayed low feeding and enzyme rate regardless of the food present.

Time acclimation of the digestive system was proposed by Mayzaud and Poulet (1978) to explain the relationship between food supply, ingestion and digestive enzyme rate. According to their hypothesis herbivorous copepods are in a more or less continuous state of being acclimated and increasing food level resulted over time in an increasing feeding rate which in turn triggers an increase in digestive enzyme synthesis. Implicit with this theory is the idea that the animals were food limited and the fact that during the survey the animals did not face drastic changes in the quality of their particulate trophic environment. Stresses related to sudden variations in the ratios of carbohydrate or lipid to protein of phytoplankton induces repression of *Acartia clausi* most inducible enzymes such as laminarinase and cellulase (Fig. 5). Amylase and alkaline proteolytic activities appeared to be less sensitive to these variations since they correlated positively ($p > 0.05$) with particulate protein and chlorophyll content respectively (Table I). Positive and significant correlations are obtained between all carbohydrases activities and the descriptors of the potential food supply when the four observations characterized by an abrupt change in the particulate C:N ratio are ommitted (Table I), confirming the

Table I. *Correlation analysis among enzyme activities and between enzyme acitvities of* A. clausi *and soluble protein content of individual copepod (Sol. proteins) as well as particulate proteins (Total proteins), carbohydrates (Total Carb.), chlorophyll* a *and total volume (TOT. VOL.). df=9;* $*=p < 0.05$; $**=p < 0.01$.

Between brackets correlation coefficients when enzyme values corresponding to drastic changes in the particulate C:N ratio were ommitted.

	Lmnase		Cellulase		Amylase		Ac. Proteases		Alk. Proteases	
Lmnase	1.000									
Cellulase	0.758**		1.000							
Amylase	0.098		0.395		1.000					
Ac. Proteases	-0.076		-0.547		-0.282		1.000			
Alk. Proteases	0.131		-0.020		-0.166		0.357		1.000	
Sol. Proteins	0.197		0.564		0.451		-0.718*		-0.484	
Total Proteins	0.067	(0.735)*	-0.001	(0.304)	0.687*	(0.718)*	0.381	(0.294)	0.447	(0.267)
Total Carb.	-0.107	(0.731)*	-0.198	(0.066)	0.242	(0.445)	0.246	(0.114)	0.516	(0 356)
Chlorophyll a	-0.157	(0.922)**	-0.003	(0.620)	0.333	(0.730)*	0.129	(-0.044)	0.650*	(0.584)
TOT. VOL.	0.093	(0.717)*	0.001	(0.282)	0.396	(0.764)*	0.395	(0.244)	0.521	(0.212)

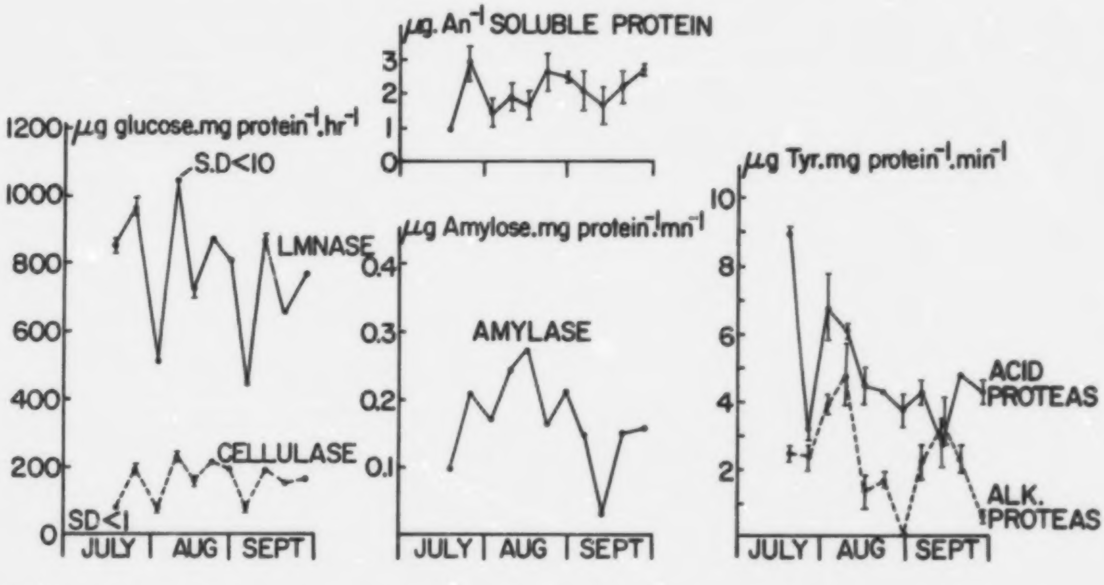

Figure 5. *Changes in digestive enzyme activities and individual soluble protein content of late stages of Acartia clausi. Taken from Mayzaud and Mayzaud (1985).*

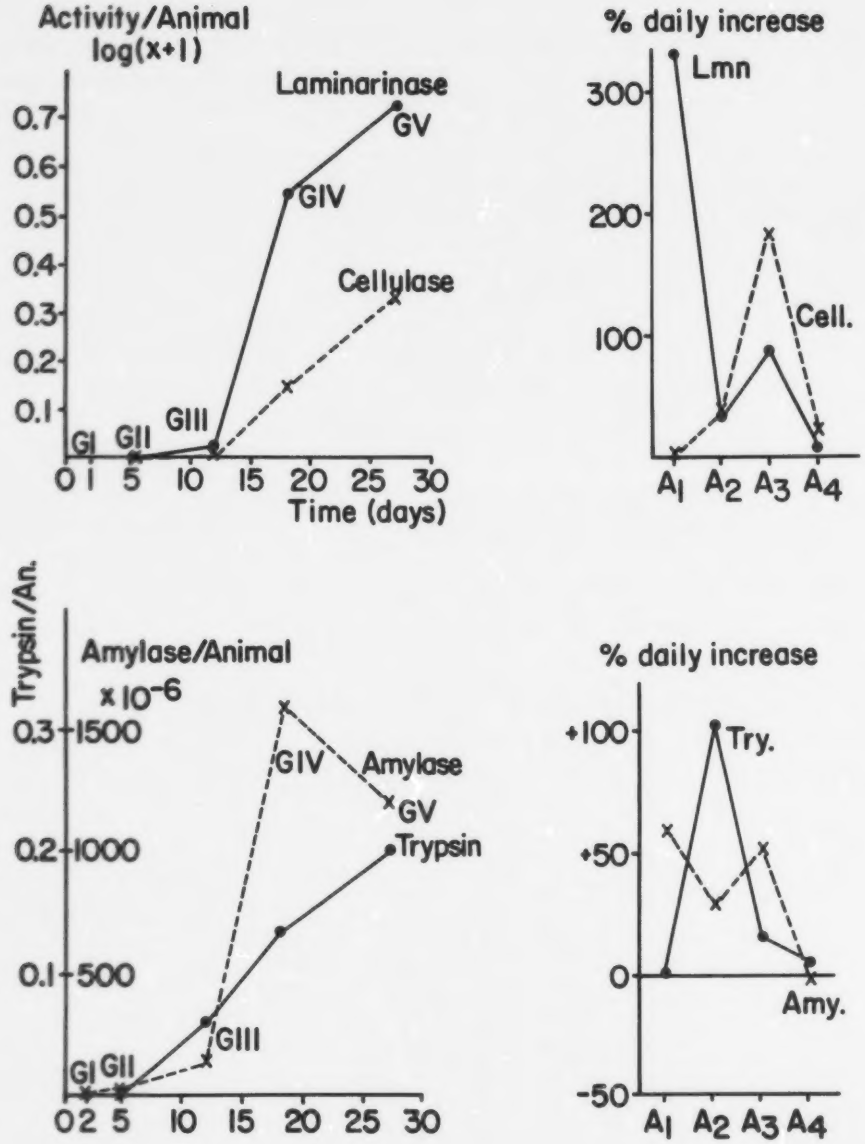

Figure 6: *Changes in carbohydrase and trypsin activities during growth and percent daily increases in Temora stylifera.*

idea that besides food quality, changes in food concentration remain an important factor of Acartia clausi digestive enzyme levels.

Long term regulation of the nutritional process.

The different patterns of enzyme changes observed by Tande and Slagstad (1982) for stage V and adult females of Calanus finmarchicus captured in the same environment, strongly suggest that metabolic requirements could also be part of the digestive enzyme regulation processes. Indeed, growth rate is directly related to the fulfillment of the metabolic needs and is associated with an appropriate food supply (Conover, 1978).

The lack of data for marine zooplankton organisms have prompted us to consider this aspect of digestive enzyme regulation with the omnivorous neritic copepods Temora longicornis raised in the laboratory with mixed phytoplankton from eggs to adults. Because of the difficulty to obtain sufficient numbers of each growth stage, several were pooled before enzyme analysis. Group I (G I) includes nauplii 1 to 3, group II (G II) includes nauplii 4 to 6, group III (G III) copepodites 1 to 3, group IV (G IV) copepodites 4 and 5 and group V (G V) adults.

The activities per animal of the four enzymes studied followed a pattern of variation similar to the one described for growth body weight (Mayzaud, O. et al., in prep.). The first naupliar stages only displayed low levels of amylase and laminarinase (Fig. 6) while the measurable activity of cellulase and trypsin began with the first copepodite stages. The absolute rates of increases for most enzymes were maximal during the copepodite stages and either leveled off (laminarinase, cellulase, trypsin) or decreased (amylase) at adult stage.

Percent daily induction was computed using the exponential fit of Winberg (1956). As expected daily amylase and laminarinase increase were maximal for the naupliar stages and showed a secondary peak for the copepodite interstage (G III-G IV) (Fig. 6). Cellulase displayed an increasing daily induction level from naupliar to copepodite stages with a maximum similar to the amylase and laminarinase one. Daily trypsin induction was maximum for the naupliar-early copepodite interstage (G II- G III) and decreased throught the growth cycle (Fig. 6). Adult stages showed a low level of daily induction for most enzyme and a level of daily repression for amylase. Lower needs and lower increases in enzyme levels of late growth stage seems fairly general and are associated with lower growth rate. Depending on the time scale considered, such association between enzyme changes and growth has important implications on the interpretation of the relationships between food level and natural or experimental enzyme induction.

CONCLUSIONS

Over its entire life cycle, an animal will face periods of drastically different metabolic needs. It is usually admitted that the early stages of growth have larger needs than the adult with a metabolism geared toward protein synthesis rather than lipid or carbohydrates. Nutrition and growth are known to be related in marine crustaceans (Mason, 1963; Van Wormhoudt, 1980; Vidal, 1980), but very little has been published on the effect of growth needs on the long term regulation of the digestive enzymes. The results obtained for the copepod Temora longicornis displayed an excellent degree of coherence between the pattern of changes of growth rate and those of the main digestive enzymes. The early stages (nauplii, joung copepodites) showed maximum daily growth rate and maximal daily enzyme induction. Depending on the time scale considered such association has important consequences on the interpretation of the relationships between food level and natural or experimental enzyme induction. The changes in food supply will essentially affect the slope of increase of the sigmoidal changes in dry weight but will not modify the shape of the functional response (Vidal, 1980). Similar modification for the most inducible enzymes can be expected, if the relationship holds for all metabolic types and all trophic situation.

Within a given growth stage, the metabolic needs are more or less constant and the influence of food supply will depend on the limiting or non limiting nature of the trophic environment. Under non-limiting or saturating conditions, optimal assimilation is already achieved and any increase in food supply will induces a repression of the enzyme stock resulting in a negative or a lack of relationship (Van Wormhoudt, 1980b, Samain et al., 1981). Under food limiting conditions the digestive enzyme system must acclimate in order to optimize food assimilation and energy expenditure. The definition of a food-limited environment, derives usually from measurements of the particulate matter standing stock and the consumers feeding rate (Poulet, 1974; Frost, 1974; Huntley, 1981). Such definition do not usually consider the possibility that different growth stages will show different global or specific requirements. Thus a given level of natural particulate matter can be limiting for certain growth stages and not for others.

Long term regulation of the digestive enzyme levels in marine zooplankton by the metabolic requirement will always be superimposed in the medium term acclimation processes described by Mayzaud and Poulet (1978). We propose that the degree of nutritional adaptability is a function of the magnitude of the metabolic needs. Under natural conditions and when the quality of food does not vary, this magnitude is more or less constant for a given stage of growth. When the food quality vary, the resulting stress induces a temporary repression of the most inducible enzymes and time is required to acclimate to the new situation. To what extent the synthesis of large amount of lipids can affect such acclimation processes has to be shown, but seems fairly likely.

The interpretation of natural or experimental changes of digestive enzyme activities of zooplankton requires a full understanding of the relationships between ingestion, digestion and assimilation and a proper definition of the time scale relevant to the physiological response studied. If the period considered is too short the changes, if any, will reflect the feeding rhythmicity. If the period is too long and encompasses too many different growth stages or pooled too many metabolic types, a loss of information will take place through confounding of several sources of regulation.

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LIFE CYCLES AND PRODUCTION OF TWO COPEPODS ON THE SCOTIAN SHELF, EASTERN CANADA

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Abstract: An under appreciated amount of synchrony occurs among life cycles of offshore copepods in eastern Canada. This allows us to affirm that Calanus finmarchicus is basically monocyclic, and that there is no simple rule relating production to body size among species. Life cycles may be genetically adapted to more northern waters whence the Scotian Shelf receives immigrant populations.

INTRODUCTION

Although it is well established that arctic and temperate marine copepods may be sufficiently synchronous to permit quite detailed analyses of their life cycles, this possibility has not been much explored in open-ocean situations. Perhaps it is assumed that patchiness and advection would destroy most cohort patterns. Here we give a brief account of the life cycles of Calanus finmarchicus (Gunnerus) and Oithona similis Claus in waters off southwestern Nova Scotia and discuss the implications for secondary production on the Scotian Shelf. These two species were chosen because of their extreme size differences (adult body mass of C. finmarchicus ca. 120 X that of O. similis according to estimates in Tremblay and Roff, 1983).

MATERIALS AND METHODS

A series of vertical net hauls were taken from just above the bottom at ca. 100 m to the surface near the centre of Brown's Bank off southwestern Nova Scotia in 1983. Two Hansen-type nets were used: one 30 cm in diameter and with a 64 μm mesh and the other 42 cm and 202 μm respectively. The hauls were not intended to be quantitative, but it is assumed that all copepodites and adults of C finmarchicus were equally retained by the coarse net, whereas all stages of O. similis and nauplii and youngest copepodites (CI and CII) of C. finmarchicus were equally retained by the fine net.

All copepodite stages and adults of C. finmarchicus were counted and measured (cephalosome lengths) in subsamples (ca. 1/15 to 1/55) depending on abundances of the coarse-net samples. The few Calanus glacialis Jaschnov were readily discriminated by size (see McLaren and Corkett 1984, their fig. 1). All copepodids and adults of O. similis were measured and nauplii were identified to species in O. similis and to stage in C. finmarchicus in subsamples (ca. 1/11 to 1/35) of the fine-net samples. As stages CI and CII were counted in the parallel fine-net and coarse-net samples, these were used to standardize proportions of younger and older stages in the two samples.

RESULTS AND DISCUSSION

The life-history pattern of C. finmarchicus proved to be quite clear. Animals of the overwintering generation (G_o in Fig. 1) had largely matured by late February. The short-lived adult males were scarce then and no young had appeared. This suggests that most adult females had been fertilized, but had not yet spawned. By mid-April nauplii were abundant and, judging from their size, some individuals of this spring generation had reached older copepodite stages (G_1 on Fig. 2). The ratio of adult (G_o, all females) to young (all G_1) in mid-April was ca. 1:50. Although a noticeable increase of adult males on 21 May (Fig. 1) suggests that these were newly matured, a displacement of old adults of G_o was not evident in size distributions (Fig. 2) until 12 June. If we assume that all adults were G_o on 21 May, the ratio of G_o to G_1 was ca. 1:10. This implies (from the ratio of 1:50 on 16 April) that survival rate of young stages was only ca. 20% of that of adults during the prior month.

From the data on Fig. 1 and 2, adults made up 8% of G_1 in mid-June, 14% in mid-July , and 12% in early August. Thus, it seems clear that a small proportion of G_1 matured in mid-June, but that the rest stayed in a resting stage or "active diapause" (Elgmork, 1980) in CV. Nevertheless, this small fraction of maturing G_1 gave rise (largely after 12 June) to a new generation, G_2. This is evident in the reappearance of younger copepodite stages in mid-July (Fig. 1) and in the clear bimodalism of size-frequency distributions in mid-July and early August (fig. 2). The rather broad stage distributions of G_2 in mid-July suggests that spawning by the adults of G_1 was protracted. Furthermore, it is probable that the new generation suffered high mortality before reaching older stages (ratio of adult G_1 to all G_2 ca. 1:13 in early August).

Again, only a small fraction of G_2 matured in summer (from Fig 1 and 2, 4% in mid-July, 7% in early August). However, judging from the size-frequency distributions (Fig. 2), most of the overwintering stock maturing as G_o would have been derived from individuals of G_2 rather than G_1.

The development of G_1 from a modal stage at NV on 16 April to CV on 21 May (Fig. 1) can readily be compared with temperature-dependent expectations. If we assume that time from hatching to middle of NV is ca. 75% of time to CI (time from hatching to beginning of NIV is ca. 50-60% of time to CI: see Corkett et al., this volume), then the time from NV to CV at $4,5^{o}$C (see Fig. 3). is ca. 38 days. This is close to the observed time of 36 days from 16 April to 21 May (Fig. 1). The broad stage distribution and obscure origin of G_2 precludes such analysis for that generation.

As noted by Tremblay (unpublished, his appendix table 9a) the numerical abundance of copepodites of C. finmarchicus on nearby shelf waters (Emerald Bank) is much larger in spring: he gives estimates of ca. $30/m^3$ in February (which would all be G_o), $1270/m^3$ in May and $600/m^3$ in June (which would be almost all G_1 in those months), $90/m^3$ in July-August, and $80/m^3$ in August (a mixture of G_1 and G_2 at these times). C. finmarchicus also makes great weight gains between later copepodite stages. Recent estimates (Williams and Lindley, 1980, their table 1) are ca. 3, 6, 16, 40, 145 and 192 ug as weights of CI through CVI (adult). Thus, production must come overwhelmingly from the late stages of G_1 in spring. For much of the year, the population is non-reproducing, although its biomass, of course, continues to be available to the system.

In contrast of C. finmarchicus, the cohort structure of O. similis was not always clear (Fig. 4). The overwintered generation (G_o) was reasonably synchronous in late February, as was the new generation (G_1) in mid-April, which is also obvious in the increased size of adult females. Since there were no eggs or nauplii, and very few short-lived males, in mid-April, the new adult females had presumably been fertilized, but had not yet spawned.

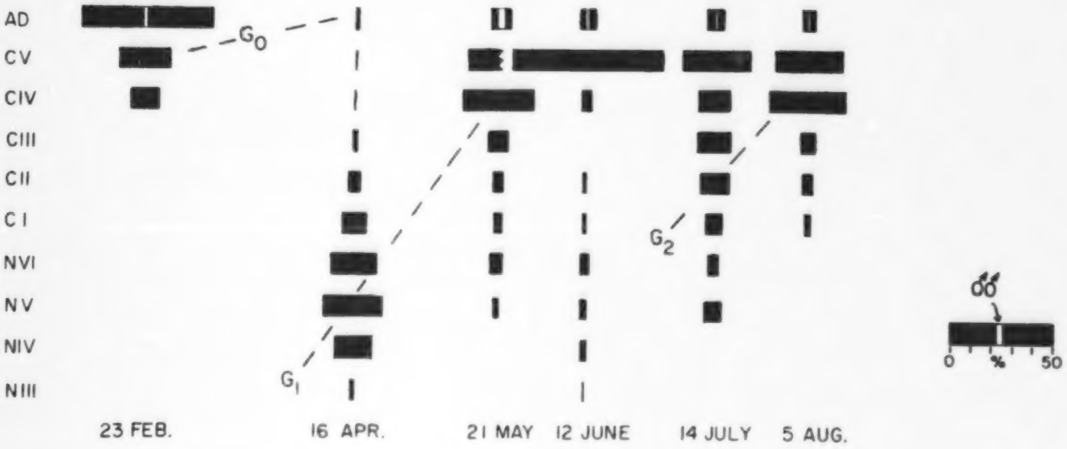

Figure 1. *Relative abundances of instars of* *Calanus finmarchicus* *in samples from Brown's Bank in 1983. Successive generations* (G_0 - G_2) *indicated (see text).*

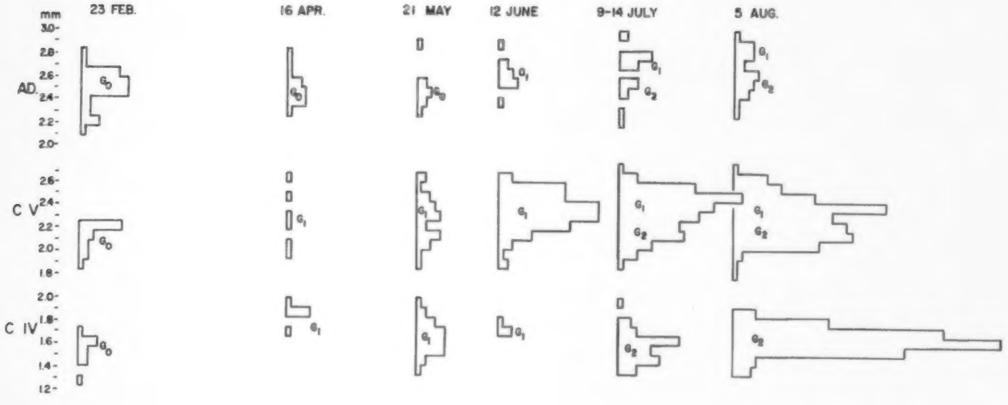

Figure 2. *Size-frequency distributions of CIV, CV, and adult* *Calanus finmarchicus* *in samples from Brown's Bank in 1983. Successive generations* (G_0 - G_2) *indicated.*

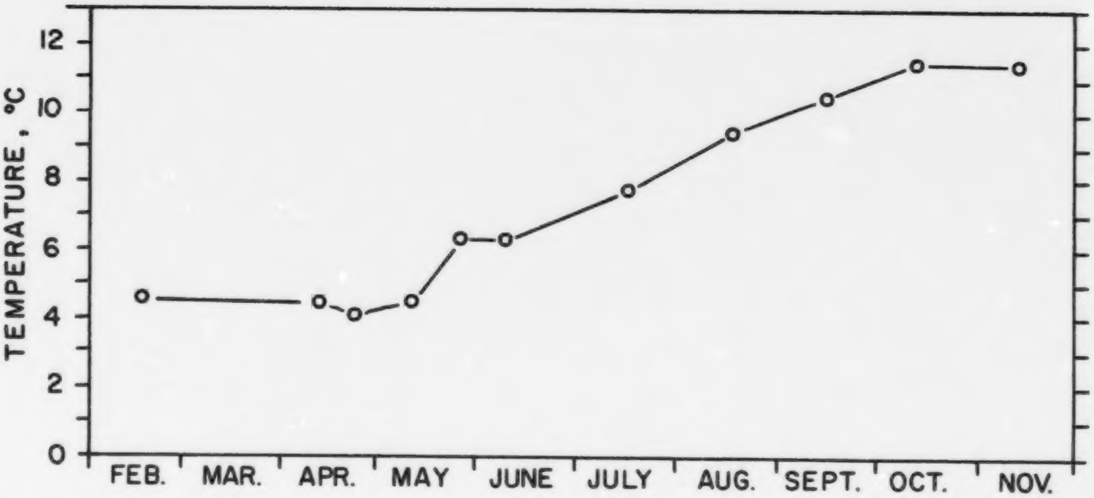

Figure 3. *Estimated temperatures on Brown's Bank during 1983. Data for Feb-June based on estimates over the bank at 10 m (courtesy of A. Koslow). Data for July-Nov based on buoy measurements N and S of the bank at 16 m (courtesy of D. Gregory).*

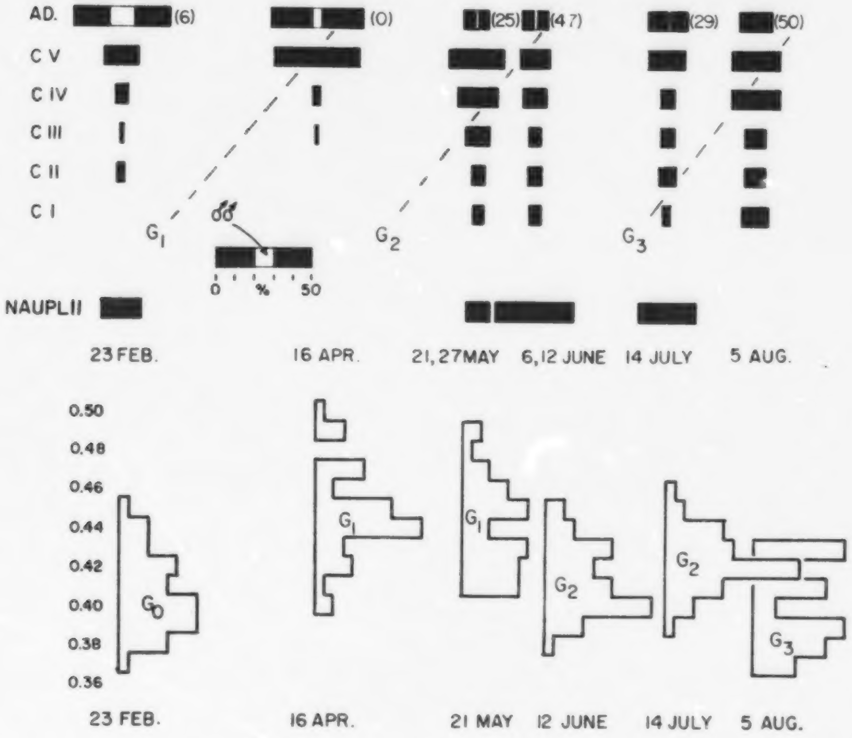

Figure 4. *Upper: relative abundances of instars of* *Oithona similis* *in samples from Brown's Bank in 1983. Numbers in brackets are the percentage of egg-bearing females (2 sacs = 1 egg bearing female). Lower: cephalosome lengths (as % of total) of adult females in the samples.*

Later samples (Fig. 4) show a considerable spread in stage distribution, implying some breakdown in cohort synchrony. Nauplii never seemed sufficiently common to supply the copepodites subsequently present. Either the fine-net samples did not in fact fully retain the very small stages, or there was heavy early mortality, or both. Nonetheless, we believe that the augmentation of copepodite stages in late May, the relative increase of adults (many ovigerous) in early June, and the distinct drop in female size in early June (Fig. 4) all herald a new generation, G_2. This generation may not have been fully recruited until later June, and there was no change in size structure in mid-July. A reinforcement of numbers of later copepodites in August, together with the initiation of a mode of smaller females (Fig. 4), is taken as indicating a new generation, G_3, which was probably not fully recruited until later August.

The fact that G_0 was so coherent in late February (Fig. 4) suggests that a period of suspended development may occur in this species during winter, although we can find no literature on this. Tremblay (unpublished, his appendix table 9a) found in coarse-net samples from Emerald Bank that there were more adults than copepodites during June through October, but that copepodites became substantially more common in November; again this suggests that development became suspended in late autumn.

Thus, assuming that another generation could have been developed between late August and late October, we conclude that there were 4 generations between late February and late October, with the fifth forming the overwintering stock, G_0 in the next year. This conclusion can be tested against the temperature-dependent generation length for O. similis, as inferred from Eaton (unpublished) by McLaren (1978). Taking a mean temperature of ca. 7^{o}C for this period (Fig. 3), we can estimate a mean generation length of ca. $12482\ (7+5)^{-2.05}$, or 76 days. This would permit about 3 generations, rather than the observed 4, during this period. Of course the match is not expected to be very close; the temperature function used by McLaren (1978) was based on very limited laboratory rearings, and O. similis may spend more time in surface waters, warmer than those used for Fig. 3. At any rate, there is no evidence for food restraints or resting stages between late February and early August and perhaps November.

In spite of its much smaller size, O. similis cannot develop potentially as rapidly as C. finmarchicus at the temperatures on the Scotian Shelf (approximated by Fig. 3). Furthermore, it has proportionately much less growth between successive stages. McLaren (1969) estimated that O. similis in a landlocked arctic fiord increased mass by ca. 1.5 times per stage (cf. 2 to 3.6 X in C. finmarchicus - see above). Most biomass and production in both species must occur in late copepodite stages. Without information on absolute numbers, it is not possible to estimate production of either species from cohort analyses. However, in spite of the greater number of generations per year in O. similis it is unlikely to exhibit the 32-fold (range 16-63) advantage in annual production/biomass ratio proposed by Tremblay and Roff (1983) on the basis of a general mass-dependent relationship proposed by Banse and Mosher (1980).

Oithona similis appears to have more-or-less continuous development for at least half the year. As a probable carnivore or omnivore (in spite of negative evidence in Eaton, unpublished) it may not have to depend directly on phytoplankton. Calanus finmarchicus, on the other hand, is clearly attuned to the spring bloom of phytoplankton. However, it is unlikely that food becomes limiting for it after the first generation, as the resting stages retain considerable lipid through the summer. (It is a little remarkable and disappointing that the only published summary of seasonal phytoplankton levels on the Scotian Shelf appears to be that prepared as part of an environmental impact statement for offshore gas exploration - see Anonymous, 1983). It might therefore be asked: why does not the entire first generation, G_1, mature in spring and give rise to a much larger G_2, which is evidently entirely responsible for producing the subsequent year's stock, G_0? We suggest that this "inefficient" life cycle is adapted to more northern waters, whence populations of C. finmarchicus are brought to the Scotian Shelf by the large-scale circulations of the western North Atlantic. Such genetically determined mismatches between copepods and their phytoplankton food may occur in many oceanic situations where extensive advection occurs.

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RÉSUMÉ

Une portion sous-estimée de synchronie apparaît dans les cycles de vie des copépodes océaniques de l'est du Canada. Calanus finmarchicus est essentiellement monocyclique bien qu'une petite fraction de la population donne naissance à une deuxième génération qui serait à l'origine des stocks de l'année suivante. Le cycle de vie de cette espèce serait génétiquement adapté aux environnements plus nordiques qui fourniraient des populations immigrantes au plateau néo-écossais. Oithona similis peut avoir 4 générations par année; cependant, son rapport annuel production/biomasse n'est probablement pas beaucoup plus élevé puisque la croissance relative entre chaque stade de développement est plus faible chez cette espèce.

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RESPONSE OF A MARINE BENTHIC COPEPOD ASSEMBLAGE TO ORGANIC ENRICHMENT

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Abstract: The study examines the impact of sewage sludge dumping on the copepod community of a subtidal muddy deposit off the Scottish coast. High levels of sedimenting sludge were found to cause marked effects on diversity, density and species composition. Three groups of species are recognized characteristic of different levels of sludge loading. Enormous densities of copepods were recorded in the most heavily polluted sediments and this is discussed in relation to the proposed use of benthic copepods in pollution monitoring programmes.

INTRODUCTION

In order to identify the structural changes in a benthic copepod assemblage of a sediment subject to high levels of organic input, a study locality was chosen which was known to exhibit a classical pattern of macrobenthic response to pollution. The dumping of sewage sludge in the Firth of Clyde on the west coast of Scotland has been taking place since 1904. Currently the operating authority is licensed to discharge up to 1.55×10^6 wet tonnes of sludge per year (192 dry tonnes per day in 1977) into a designated disposal area of 6 km^2 (Pearson, in press). The water depth in the disposal area is 70-80 m and the sediment a uniform fine brown silt. Bottom water movements are very slight and this site has been generally recognized as an accumulating dumping ground; indeed, Pearson (in press) has calculated that carbon input to the sediments over an area of 10 km^2 around the dumping ground is one to two orders of magnitude higher than the highest levels of natural carbon input to inshore sediments, and this has led to a sludge depth of 15 cm in the centre of the dumping ground.

METHODS

Sediment cores of 25.52 cm^2 were taken by Craib corer at 56 stations throughout the area during 6th-11th June 1981 (Fig. 1) and redox potential profiles down the upper sediment column recorded. Organic carbon analysis was performed on cores from 26 of these sites using a Perkin-Elmer elemental analyser, following removal of carbonate carbon. Oxygen levels in the water immediately overlying the sediment surface were measured, using the Winkler method, in samples taken from the centre of the dumping ground and at increasing distances from the centre.

Duplicate 5 cm cores for meiofaunal analysis were taken at 14 stations along a 10 km transect running north-south through the dumping ground on 6th June 1981. Meiofauna passing through a 1000 μm sieve but retained on a 63 μm sieve was extracted by floatation with Ludox (a colloidal silica manufactured by Du Pont) at a density of 1.115 g ml^{-1}. Total numbers of copepods in each core were

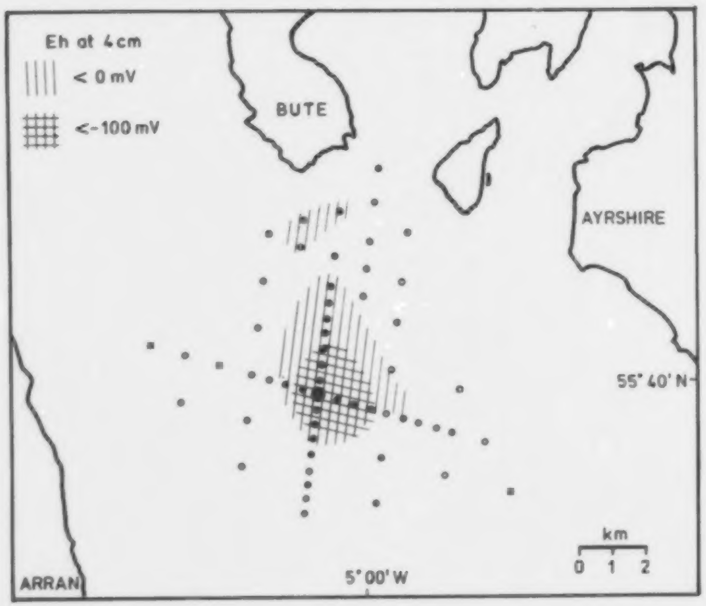
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Figure 1: *Firth of Clyde, showing sediment redox potential at a depth of 4 cm. Circles indicate core sample sites. Filled circles along the main north/south transect are sites sampled for meiofauna. The central, larger, filled circle marks the centre of the sewage sludge discharge.*

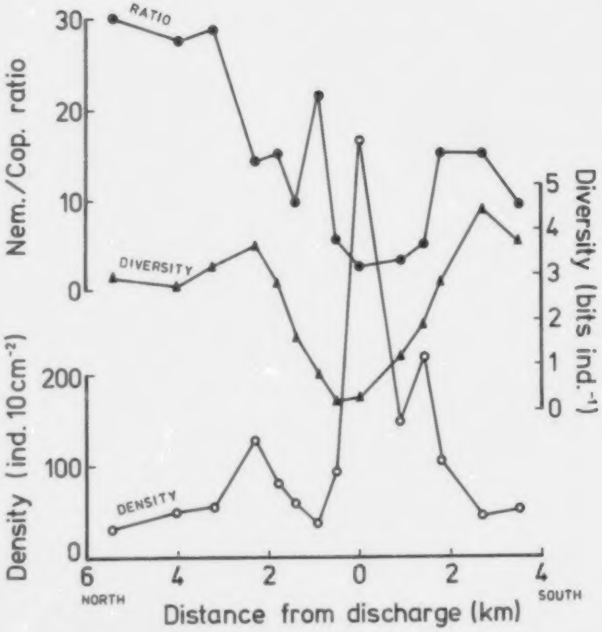

Figure 2: *Density and diversity of benthic copepods and the ratio of nematode/copepod densities along a transect passing through the Firth of Clyde - sludge dumping ground.*

determined and the species composition of the copepods in one core from each station. In fact, other meiobenthic taxa were also enumerated but this paper will concern only the copepod fraction.

RESULTS

Sludge dumping has clearly given rise to an area of seabed of low redox potential (Fig. 1). At the centre of the dumping ground 5 km² of seabed exhibit Eh values below -100 mV. Eh values rise with distance from the dumping ground but fall once again at the northern end of the transect. Carbon values show a similar pattern with the transect stations within 1 km of the centre of the dumping ground having a carbon content in excess of 5 %. Water overlying the sediment was found to be fully oxygenated throughout the area.

In the highly organic, reduced sediments, over a distance of about 5 km, copepod density is elevated (Fig. 2). In the centre of the dumping ground copepod densities are amongst the highest ever recorded for subtidal sediments, the maximum density for a single core being 782 ind. 10 cm^{-2}. Fig. 2. is suggestive of a major central peak with two minor peaks some 1.5-2 km north and south of the dump centre; however, although sample size was large by meiofaunal standards, replicate core counts were highly variable at the positions of the density peaks.

There is a marked diversity sag for about 4 km on passing through the dumping ground (Fig. 2). Diversity appears to peak towards the edges of the dumping ground, before falling slightly to presumably background levels. Species richness and evenness show similar patterns.

There is a clear succession of harpacticoid species with increasing distance from the discharge point. It is possible to recognize 3 broad groups of species which have different responses to dumping. The first group contains just 1 species. Bulbamphiascus imus flourishes in the centre of the dumping ground and is virtually the only copepod here. The second group of species includes those which are virtually absent from the centre of the ground but become dominant in the moderately enriched sediments to either side (e.g. Amphiascoides debilis?, Typhlamphiascus lamellifer, Paramphiascoides hyperborea). A third group of species only begins to appear towards the ends of the transect (e.g. Pseudameira furcata, Pseudameira sp., Amphiascoides subdebilis).

DISCUSSION

An enhancement of copepod density resulting from sewage pollution has also been observed by Vidakovic (1983), although a reduction has been more generally observed (e.g. McIntyre, 1977; Raffaelli and Mason, 1981; Amjad and Gray, 1983). On consideration of the macrofaunal response to organic enrichment, a varied response by harpacticoids might be expected, being dependent upon the level of enrichment and the degree of inimical chemical changes. In view of this varied response we can question the validity of the employment of the ratio of nematode to copepod densities as a pollution monitoring tool, with high values indicating pollution (Raffaelli and Mason, 1981). Fig. 2 shows the change in this ratio along the dumping ground transect and, despite variation between replicate cores at some sites, ratios are clearly lowest (about 3:1) in the most polluted sediments. As regards sewage-contaminated waters, this agrees with the findings of Vidakovic (1983) but is opposite to those of Raffaelli and Mason (1981) and Amjad and Gray (1983). It is likely that the ratio is strongly influenced by the availability of high dissolved oxygen levels to the copepod fauna. Thus in the present case and in Vidakovic's (1983) study the overlying water contained high levels of dissolved oxygen. Although at the centre of the dumping ground the sediment interstitial water would be low in oxygen and high in hydrogen sulphide, the dominant species, Bulbamphiascus imus, has been observed in culture to make frequent excursions to the sediment surface, where a high oxygen tension is readily available. In Amjad and Gray's (1983) study in Oslofjord low copepod densities and high nematode: copepod ratios corresponded with low oxygen levels in the overlying water. On the polluted beaches of Raffaelli and Mason (1981) the availability of high dissolved oxygen levels in the overlying water would be reduced to the period of immersion of their sites whilst during the period of emmersion the harpacticoids will have no means of avoiding conditions of low oxygen and high sulphide which may develop. Thus it is worth emphasizing that the nematode/copepod ratio will be influenced by water quality both within the sediment and in the overlying water and the influence of the latter will be greater subtidally and towards the bottom of the shore, where it may mitigate adverse sedimentary conditions.

Fig. 2 would suggest a pattern of diversity variation along a gradient of organic enrichment similar to that commonly observed for macrofaunal species (Pearson and Rosenberg, 1978): thus on moving towards cleaner sediments, a rise in diversity occurs with a peak in moderately enriched sediments and thereafter a decline to diversity values typical of clean sediments. Whilst this may indeed be the case for the southern arm of the transect, diversity along the northern arm remains low, particularly when compared with diversity values derived using the same methods for similar depths and sediments a little farther south in the Irish Sea (Moore, 1979). The northernmost station corresponds approximately to the location of a pre-1976 sludge dumping ground and to an area of low redox potential (Fig. 1). and so it seems likely that purification of the sediments here has not been fully completed.

Several workers have examined the impact of sewage on harpacticoid species composition but the most comparable study is that of Marcotte and Coull (1974) who examined the effect of a sewage outfall discharging into shallower water but in a region of the Mediterranean of similar salinity and sediment type. They too recorded an overwhelming dominance of Bulbamphiascus imus at their most polluted station in summer, although in winter this species was replaced by Tisbe sp. The eurytopic B. imus is not generally dominant in sublittoral silty sediments and so its dominance may be a corollary of high organic levels in silty sediments. Its large size and abundance would indicate that it could be a very important carbon assimilator in organically enriched areas.

RÉSUMÉ

Les niveaux élevés des vidanges avaient un effet profond sur la densité, la diversité et la composition d'espèces de copépode harpacticoide benthique dans le Firth de Clyde en Écosse. Trois groupes d'espèces sont présentés qui characterisent des niveaux différentes de vidanges. Une densité énorme de copépode a été noté pour les sediments le plus pollué. Ceci est discuté par rapport a l'utilisation des copépodes pour les observations sur la pollution.

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TEMPERATURE-DEPENDENT CHANGES IN COPEPOD ADULT SIZE: AN EVOLUTIONARY THEORY

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Abstract: Adult size generally decreases with increasing temperature for copepods. It is shown that if growth rates increase with temperature then the hypothesis of adaptation implies that mortality rates must increase as fast or faster than growth rates increase with temperature. Evidence is presented for such an increase.

INTRODUCTION

Within populations of copepods, adult size typically increases as the seasonal environmental temperature decreases (Deevey, 1960; McLaren, 1963). An apparent exception is reported for an harpacticoid copepod by Evans and Diaz (1978), but that report lacks cohort data and possibly the larger early summer adults could have matured at winter temperatures. The hypothesis that this is an adaptive response to a changing environment is examined here using inverse optimization techniques (Myers and Doyle, 1983; Myers and Runge, 1983) to make quantitative predictions of the environmetal conditions under which an increase in size at maturation is adaptive. An alternative hypothesis is that such changes in adult size are not evolutionary adaptations, but are the result of physiological, biochemical or thermodynamic constraints. It has been suggested (Ray, 1960) that such a constraint may be the limitation imposed by requiring enzymes to function over a wide temperature range, even through examples of temperature dependent expression of enzymes are well known. The hypothesis of constraint is examined by Runge and Myers in this volume.

It is possible that the dichotomy between "constraint" and adaptation is more apparent than real. That is, there may exist additive genetic variation in the population that in time would allow maturation at the same size over a range of temperatures. However, the detrimental pleiotropic effects from such a change (e.g. a reduction in growth rate) may prevent such genetic variation from responding to natural selection.

Since growth rates and egg production rates generally increase with size for copepods (e.g. Corkett and McLaren, 1978) it is not true that natural selection acts such that adult body size is "optimized" at the size that energy available for growth and reproduction per unit time is maximized. Thus, changes in mortality must be included in any calculation of fitness and a dynamic optimization approach is needed, and is used here, to determine fitness (Myers and Doyle, 1983).

The fundamental empirical observation used here is that individual growth generally increases with temperature (within the temperature range in which the animal occurs) in the field or under laboratory conditions if adequate food supply is available (reviewed in Hartnoll, 1982). If growth rate increases, and yet adult size remains the same (or decreases), then it is shown in the appendix that mortality rate must increase at a greater rate than the increase in growth rate. (The result in the appendix is for a special case, e.g. constant mortality; more general results will be discussed elsewhere).

The principal conclusion from the appendix is thus that mortality rates must change in concert with growth rates for populations of copepods if size at maturation remained the same at all temperatures. Specifically, if two populations are alike except for mortality rates and growth rates, then the ratio of the growth rates, (the greater over the lesser) is less than the ratio of the mortality rates. Although the reasoning for this is not readily evident in the mathematics of the appendix, the proposition is basically true because an increase in energy available for growth and reproduction results in roughly a multiplicative increase in the ability to produce eggs, whereas an increase in mortality results roughly in an exponential decrease. If size at maturation decreases with increasing temperature, as is observed, then mortality must increase even faster with increasing temperature if the change in size at maturation is adaptive.

The definition of fitness used in the appendix is an approximation because nonstable age-structures, and genotypic and phenotypic variability in the life-history traits both exist and are not explained by the maximization process assumed. There is no *a priori* reason to believe that either effect will lead to a systematic bias in our results. Tests of the predictions of our theory are partially tests of the adequacy of the model in the appendix to explain the evolution of size in copepods.

An important complication relevant to our analysis is that age at senescence decreases with increased temperature. In the appendix, age at senescence was assumed constant. This complication was taken into account in the analysis of the copepod *Acartia clausi* discussed in Myers and Runge (1983). The predicted and observed slope of mortaliy vs. temperature (.0151; s.e. = .00197 and .0144; s.e. = .00644 respectively) are approximately equal to the observed slope of the growth rate temperature relationship (.0143; s.e. = .00122). Thus, at least for *A. clausi*, this complication changes the theoretical prediction of the model slightly. Growth rate and mortality rate are still coupled with temperature, but the differences between the slopes of growth rate and mortality rate with temperature are less.

We have not discussed changes in size-specific mortality. Although such changes certainly exist, this is essentially a specialized version of the proposed coupling between temperature and mortality that is difficult to evaluate with the data presently available.

The hypothesis of adaptation can be rejected if the observed seasonal mortalities contradict the predicted "adaptational" mortalities. Although mortality generally increases with temperature, whether it increases sufficiently to make observed sizes at maturation adaptive is an empirical question that can only be answered with meticulous field measurements of life-history characteristics and natural mortality rates. Landry's (1978) research on the population dynamics of *A. clausi* may be the most comprehensive in this regard; the adaptational hypothesis was sufficient to account for this data (Myers and Runge, 1983).

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APPENDIX

Proposition

Consider an animal whose growth in dry weight ($w(t)$) and reproductive schedules $m(t)$ by age t are given by

$$\frac{dw}{dt} = (1-\mu(t))\alpha w(t) \tag{A1}$$

$$m(t) = C_e\mu(t)\alpha w(t) \tag{A2}$$

where $u(t)$ is the proportion of energy available for growth and reproduction, $\alpha w(t)$, that goes into reproduction. Restrict the control variable $\mu(t)$ such that $0 \leq \mu(t) \leq 1$. The growth rate, α, and egg energy content, C_e, are assumed constant. If the population growth rate is zero, the appropriate measure of fitness is

$$\int_0^T \exp(-\mu t)m(t)dt, \tag{A3}$$

(Charlesworth, 1980), where $\exp(-\mu t)$ is the probalility of surviving to age t and T is the age of senescence, i.e. the age at which survival and egg production drastically decreases. **For an animal that matures at the same size at two different growth, fitness can be maximized in both cases only if mortality increases at a greater rate than growth (α).**

Proof

The control problem specified by A1-A3 can be solved via Pontryagin's Maximum Principle (Pontryagin et al., 1962). For a given α and μ the functional A3 is maximized if $\mu(t)$ changes from 0 to 1 at time given by

$$\tau = T - (1/\mu)\ln\left(\frac{\alpha}{\alpha - \mu}\right), \tag{A4}$$

i.e. τ is the optimal age at maturation and $w(\tau)$ is the adult weight. Since a directly analogous problem was solved by Macevicz and Oster (1976) the details of the above derivation will not be given here. Consider a second growth rate α' such that $\alpha' = \alpha\delta$, where δ is greater than one. For α' the new optimal age at maturation, τ' can be determined using A4 for any new mortality rate μ'. For an animal to mature at the same size at two different growth rates $\alpha\tau$ must equal $\alpha'\tau'$. Using this requirement and A4 we can write an implicit equation for μ'

$$(1-\delta)T = (1/\mu)\ln\left(\frac{\alpha}{\alpha-\mu}\right)-(\delta/u')\ln\left(\frac{\alpha}{\alpha-\mu'/\delta}\right). \qquad \text{(A5)}$$

I wish to show that

$$\mu' > u\delta\text{, if } \delta > 1. \qquad \text{(A6)}$$

Note that if δ is greater than one then the left hand side of A5 is negative. Note also that if μ' is less than or equal to $\mu\delta$, then the right hand size of A5 is positive. Thus, condition A6 must be true and the proposition is proved.

THE WIDESPREAD OCCURRENCE OF COPEPOD-BACTERIAL ASSOCIATIONS IN COASTAL WATERS

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Abstract: The copepod Acartia clausi Giesbrecht is an important component of the zooplankton in coastal waters along the coasts of Japan, Europe, Britain and the United States. Bacterial colonization on the exoskeleton of A. clausi and A. longiremis was examined by SEM on samples obtained from 5 different coastal waters. Bacteria attached to the copepods were observed mostly in the depressed parts of the ventral side; near the base of the antennules, antennae, mandibles and around the labrum. The percentage occurrence of copepods with bacteria ranged from 0.3 to 29% in Tokyo Bay (Japan), 0.7 to 5.2% in the Po estuary (Italy), 0.4 to 3.5% in Miramare (Italy) and 0.6 to 1.7% in Bay of Naples (Italy). A. longiremis in Helgoland waters had higher percentage of bacterial attachment than A. clausi in Tokyo Bay. Thus, bacterial colonization of copepods is a global phenomenon in marine coastal areas. The occurrence of copepods with bacteria is especially common in eutrophic waters such as Tokyo Bay. These bacterial infections may lead to a shortening of copepod life span and a decrease in survival rate. Therefore, it is important to estimate the effects of bacterial colonization on living copepods.

INTRODUCTION

Some bacteria are attached to plankton and other small particles in the sea-water, although these attached bacteria fluctuate in number geographically, vertically and seasonally. The number of attached bacteria accounted for less than a few percent of total bacteria (total count, TC) in the open ocean (Hobbie et al, 1972). In contrast, the percentage of attached bacteria ranged from 9.0 to 35% of TC in the eutrophic environment of Tokyo Bay (Fukami et al., 1983). Based on the difference between the taxonomic composition of bacteria from zooplankton and sea-water samples, Simidu et al. (1971) suggested that Vibrio and Aeromonas are closely associated with marine organisms, in particular animals. Sochard et al. (1979) demonstrated that marine copepods carry a bacterial flora both on their surfaces and in their guts, the predominant bacteria being the genus Vibrio. Examination of copepods collected from the Patuxent River and incubated for 36 hrs in flasks inoculated with bacterial cultures revealed that Vibrio cholerae attached to the live copepods, with selective attachment taking place on the copepod surface (Huq et al., 1983). Nagasawa et al. (in press) demonstrated that bacterial colonization occurs on the surface of the copepod, Acartia clausi, collected from Shinhamako, a saline lake connected to Tokyo Bay, and that such copepods accounted for 9 to 30% of the population in January and April 1983, respectively.

The present study was carried out to confirm that the occurrence of bacteria on living copepods is common in several coastal areas.

MATERIALS AND METHODS

Plankton samples used in this study were obtained from 3 stations in Tokyo Bay on 5 different dates. Water temperature, salinity and chemical oxygen demand (COD) were measured (Table 1). In

Table 1. *Percentage of copepods with bacteria, water temperature, salinity and COD at depth of 10 m from Tokyo Bay. *: Figures in parentheses indicate numbers of copepods examined.*

Date 1983	Percentage of copepods with bacteria*(%)			T(°C)			S (°/oo)			COD (ppm)		
Stat.No.	1	2	3	1	2	3	1	2	3	1	2	3
Jan. 13	0 (232)	0 (202)	1.2 (247)	11.7	12.4	12.6	32.39	32.59	32.88	1.28	1.13	1.06
Feb. 1	0.9 (334)	0.3 (313)	2.1 (235)	10.9	11.1	11.9	32.56	32.73	33.06	1.31	1.28	1.21
Mar. 1	7.1 (268)	6.2 (355)	18.8 (208)	9.4	9.5	10.3	32.31	32.39	32.95	1.61	1.24	1.08
Apr. 5	15.7 (127)	22.3 (139)	29.1 (179)	11.7	12.2	12.5	32.11	32.47	33.17	1.35	1.27	1.11
Jul. 4	10.9 (211)	12.8 (250)	0 (265)	20.9	21.2	21.0	31.31	30.83	31.99	1.39	1.90	1.52

Table 2. *Percentage occurrence of copepods with bacteria in different areas in Europe.*

Area	Date	Stat. No.	No. of copepods examined	Percentage colonized by bacteria in %
Mediterranean Sea	June 16, 1983	1	104	1.0
	June 16, 1983	2	138	0.7
	June 16, 1983	3	116	0.9
Bay of Naples	June 16, 1983	4	120	0
	June 16, 1983	5	98	0
	June 16, 1983	6	179	1.7
	June 16, 1983	7	177	0.6
Adriatic Sea	Sept. 1979	C1	137	0.7
	Sept. 1979	C4	122	2.5
Po estuary	Sept. 1979	E2	200	1.5
	Sept. 1979	E4	211	5.2
	May 08, 1970	1	247	0.4
near Miramare	July 15, 1970	1	144	3.5
	Sept. 22, 1970	1	249	0.4
	Nov. 24, 1970	1	250	1.6
North Sea	Sept. 13, 1983	1	163	28.8
Helgoland	Sept. 15, 1983	1	163	37.4

addition, copepods obtained from 4 different areas were used to see if bacterial colonization is common in other coastal areas, namely the Bay of Naples (Mediterranean Sea), the Po estuary (Adriatic Sea), Miramare (Adriatic Sea) and Helgoland (North Sea).

Adults of A. clausi or A. longiremis were removed from the preserved plankton samples and examined in a JSM-35 scanning electron microscope following the preparation procedure described by Nagasawa et al. (in press). The numbers of copepods examined are indicated in Tables 1 and 2. Although some copepods had large numbers of bacteria and others had a small number of bacteria, only the percentages of copepods with and without bacteria will be discussed here.

RESULTS

Attachment of bacteria to copepods was selective since the heaviest concentrations of bacteria were observed in the depressed parts of the ventral side. Bacteria were often found near the base of antennules, antennae, mandibles, and around the labrum in specimens obtained from all areas (Fig. 1). Bacterial attachment was seldom observed in the joints of segments and legs, and on the legs themselves of Helgoland samples (Fig. 1), unlike the observations of Nagasawa et al. (in press). The number of bacteria found was variable and ranged from zero to large numbers (Fig. 1). Thus it is necessary to examine numerous specimens from multiple samples collected at different stations on the same date in order to determine the degree of bacterial attachment (Tables 1 and 2).

In Tokyo Bay the percentage of copepods with bacteria (CWB) was very low in January and February, being not significant at the 1% level. In contrast, in March, April and July the difference in percentage of CWB was significant at the 1% level at the three stations. The percentage of CWB increased from January through April. The April samples had the highest percentage despite little change in environmental factors such as temperature, salinity and COD (Table 1). In July bacterial colonization of copepods decreased. On the whole, the difference in percentage of CWB at each station was seasonally significant at the 1% level.

The percentage occurrence of CWB may depend on the number and species of bacteria occurring in the sea. Although the species of bacteria associated with copepods were not determined, it is likely that species of Vibrio are present in these colonies of bacteria as Nagasawa et al. (in press) suggested. In January and July red tide occurred at the time of plankton collection. This red tide was caused by Skeletonema costatum (Grev.) Cleve, whereas in July the dominant element of the red tide was Navicula sp. We frequently found copepods carrying chains of S. costatum in their mandibles and swimming legs in the January samples (Fig. 1). Kogure et al. (1979) demonstrated that the growth of Vibrio was inhibited by S. costatum in mixed cultures. If the assumption that species of Vibrio are present in bacteria attached to copepods is correct, the growth of Vibrio would be suppressed by the presence of abundant S. costatum. Thus in January bacterial attachment to copepods occurred infrequently due to the small number of Vibrio during the S. costatum bloom.

The percentage occurrence of CWB in other areas is shown in Table 2. These data suggest that bacterial colonization of copepods is a widespread phenomenon in eutrophic coastal waters. The Bay of Naples, Po estuary and Miramare samples had relatively low percentages of bacterial attachment to copepods, while the Helgoland samples had relatively high percentages (Table 2). Samples from each area had percentages which are not significant at the 1% level. Therefore, no seasonal variation of

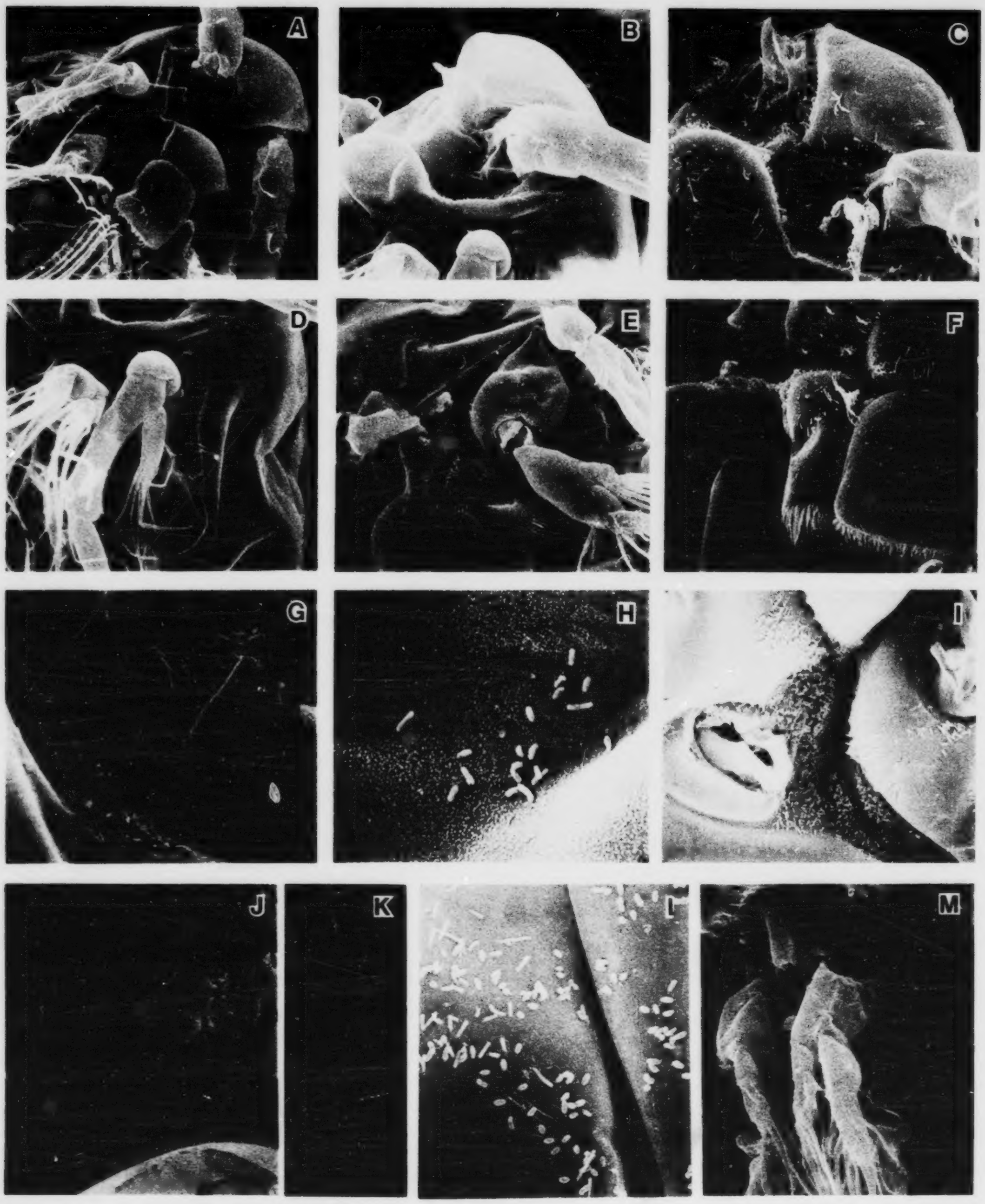

Figure 1. *Scanning electron micrographs of copepods (A-L Acartia clausi; M, A. longiremis) free of bacteria (A) and those associated with bacteria (B-M). Specimens obtained from Tokyo Bay were used for the pictures (A-I), whereas those obtained from Bay of Naples, Miramare, Po estuary and Helgoland were used for J, K, L and M, respectively. (A) This specimen has chains of Skeletonema costatum near mouth. x 180. (B-F) Ventral view of five different specimens associated with bacteria. (B) x 288. (C) x 360. (D) x 288. (E) x 240. (F) x 396. (G-I) Variations in the number of bacteria. (G) x 3600. (H) x 240. (I) x 720. (J) Bacteria found near the base of antenna. x 1800. (K) Bacteria found near the base of antennule. x 1800. (L) Lateral side of joint of segment is colonized by bacteria. x 2400. (M) Colonies of bacteria are found on the segments and swimming legs. x 324.*

bacterial attachment was observed in Miramare unlike in Tokyo Bay. The Helgoland samples contained A. longiremis, not A. clausi.

DISCUSSION

According to Uye (1982) the generation time of A. clausi is about 30 and 40 days at water temperatures of 11-14 and 9-10°C, respectively. Judging from water temperatures in Tokyo Bay (Table 1), specimens obtained in different months probably belong to different cohorts. Uye (1982) estimated, that the ecological longevity of adult A. clausi ranged from 1.4 to 9.8 days whereas the physiological adult longevities ranged from 27 to 68 days. This suggests that the adults suffer from severe predation in the sea. In addition, the present study revealed that adult copepods are often colonized by bacteria which may affect their survival rate and ecological longevity. If severe predation also takes place in copepods with bacteria, bacteria will be transferred to carnivores, such as chaetognaths and medusae.

Data available on viable bacterial counts and microflora in the areas studied are very few. Vibrionaceae accounted for 20 to 40% of bacterial flora in Tokyo Bay in 1964 to 1965 (Kaneko et al, 1969), whereas Vibrionaceae were few or absent in the inner parts of this bay in 1972 (Simidu et al. 1977). Such a change in bacterial flora suggests the advance of eutrophication in Tokyo Bay. In general, the abundance of Vibrionaceae is low in the sea-water of eutrophic areas such as Tokyo Bay and Osaka Bay (Simidu and Taga, 1980). This may be due to the attachment of Vibrionaceae to copepods and other zooplankton as suggested by Simidu et al. (1971).

This study also revealed that the percentage occurrence of copepods with bacteria changes seasonally in Tokyo Bay, suggesting changes in numerical and ecological relationships between Vibrio, S. costatum and copepods. Analyses of important relations between copepods and bacteria require further investigation, including identification of the bacteria and the effects on bacterial infection of live copepods.

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STRUCTURE AND FUNCTION OF THE CEPHALOSOME-FLAP ORGAN IN THE FAMILY OITHONIDAE (COPEPODA, CYCLOPOIDA)

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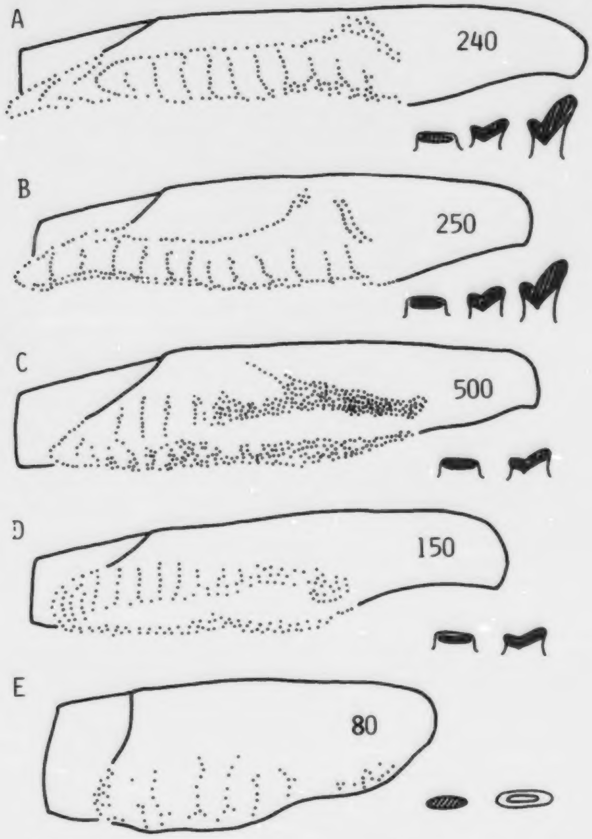
Abstract: SEM and TEM observations revealed a unique structure around the lateral flap of the cephalosome in the family Oithonidae. This structure, named "the cephalosome-flap organ (CFO)" provisionally, is composed of a well developed arrangement of pores first described by Ferrari (1977) and a pair of hairs protruding from each pore. CFO was found in the adult male of the genus Oithona. In O. davisae the diameter of the hair is about 0.5 μm while the length is about 30-40 μm. Each hair has a ciliary structure with 50-60 microtubules at the level of the pore. The structure of CFO, the mating behavior and lack of complex copulatory appendages in the oithonids suggest that it may function as a chemical and/or mechanical sensory organ in mating behavior.

INTRODUCTION

Various types of organs exist on the integument of pelagic copepods (Fleminger, 1973). Ferrari (1977) first described the complex group of integumental organs in the cephalosome of the cyclopoid genus Oithona and suggested the importance of this character in the male taxonomy. Later he expanded his research to include the neritic species from various geographic areas, found similar types of "pore signatures" common in the genus and stressed the necessity to study the biological role of this character. I have named this character "the cephalosome-flap organ (CFO)" provisionally, assuming that it represents an organ with a certain function. This paper examines the generality of CFO in Oithonidae and its ultrastructure with a discussion of its biological significance.

MATERIALS AND METHODS

The types of pore signature were examined on the specimens of 12 species of Oithona (Fig. 1), Paroithona sp. and Cyclops vicinus deposited in the Ocean Research Institute. They were fixed and preserved in 2-4% formaldehyde buffered with sodium tetraborate. The adult males were dehydrated through a graded series of ethylalcohol, critical-point dried, coated with gold and examined with a scanning electron microscope (SEM). Ultrastructure of the CFO was examined on the specimens of Oithona davisae collected in Tokyo Bay. Live specimens of adult and copepodid-V males were fixed in Karnovsky's fixative and post-fixed in 1% OsO_4. Both fixatives were in 0.1M Millonig's phosphate buffer. Some of these specimens were dehydrated and critical-point dried for SEM observation. The others were dehydrated and embedded in Epon 812. Thin sections were stained with uranyl acetate and lead citrate and examined with a transmission electron microscope.



	SPECIES	
TYPES OF PORE SIGNATURE AND MARGINAL PROCESS	LITERATURE RECORDS	PRESENT STUDY
A	*Oithona plumifera* *O*. sp.3 *O*. sp.4	*O*. *atlantica* (1) *O*. *decipiens* (3) *O*. *plumifera* (12) *O*. *setigera* (8) *O*. *similis* (7)
B	*O*. *dissimilis* *O*. *hebes* *O*. *wellershausi* *O*. *brevicornis* *O*. *amazonica* *O*. *fonsecae*	*O*. *davisae* (7) *O*. *brevicornis* (2)
C	*O*. sp.2	*O*. *robusta* (11)
D	*O*. *nana*	*O*. *nana* (9)
E	*O*. *simplex*	*O*. *simplex* (5)

Figure 1. *Five types of pore signature and marginal process found in the adult male of the genus Oithona. Approximate number of pores in one side of cephalosome is indicated at the head region of each figure. Literature records are from Ferrari (1977, 1981) and Ferrari and Bowman (1980). The numbers of specimens examined in the present study are indicated in parentheses.*

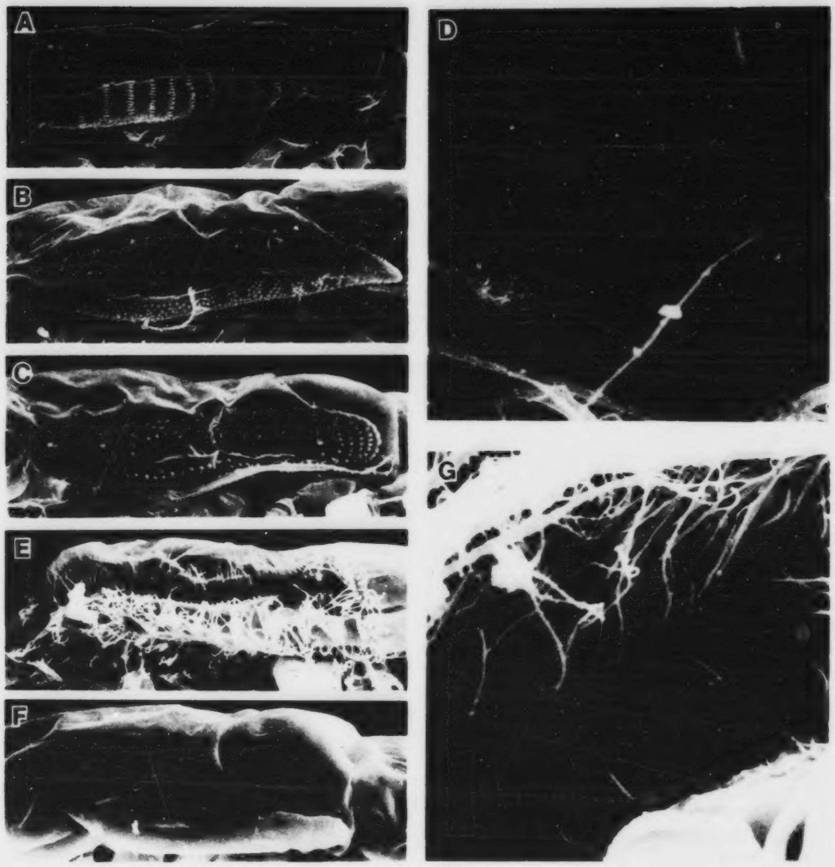


Figure 2. *Lateral views of cephalosome in different species. A, Oithona setigera, x 247; B, O. robusta, x 228; C, O. nana, x 513,; D, O. simplex, x 2470; E, O. davisae, x 570; F, O. davisae (copepodid-V male), x 627; G, O. davisae, x 3040. Specimens A-D were fixed with formaldehyde, E-G with Karnovsky's fixative and* OsO_4.

RESULTS

The pore signature was absent in the specimens of Paroithona sp., Cyclops vicinus, Oithona oculata and O. rigida, but present in all the other species examined. In the former four species only a few small pores as described for O. oculata and O. bjornbergae (Ferrari and Bowman, 1980) were present on the lateral surface of the cephalosome. The pore signatures are grouped into five types (Figs. 1, 2A-E), representatives of which have been described by Ferrari (1977, 1981) and Ferrari and Bowman (1980). SEM observation of O. davisae fixed with Karnovsky's fixative and OsO_4 showed a pair of slender hairs protruding from each pore (Fig. 2G). These hairs can also be observed in live specimens under a light microscope. The diameter of hairs is about 0.5 μm at the level of the pore while length is about 30-40 um. The copepodid-V male has flaps without a pore signature (Fig. 2F).

The internal structure of CFO is shown in Fig. 3. The two hairs protruding from each cuticular pore run into a spherical cavity in the body trunk through a narrow path. It seems that all the spherical cavities are located in the trunk of cephalosome, not the flap, because the inside of the flap is filled only with the microtubule bundles and enveloping cells (Fig. 3B). The basal part of "the hair" (hereafter referred to as "the cilium") displays a ciliary structure of 9+0 pattern (Fig. 3H). Basally the ciliary microtubules connect with one basal body and rootlet. This part of the cilium is swollen with many microvilli which fill the space of the cavity, and partly connect to a cell, which encloses the cavity, by septate junctions (Fig. 3I). It is unknown whether all the microvilli in the cavity are derived from the basal swelling of the cilium, or a part of them are from the enveloping cell. So far I have been unable to obtain sections proximal to the basal-body region. At the level of the narrow path near the spherical cavity, the cilium loses its 9+0 pattern and becomes a bundle of five microtubules (Fig. 3G). The number of microtubules increases distally, being 50-60 at the level of the cuticular pore and 60-100 more distally (Fig. 3D). The cilia are not branched. They are enclosed by one or more enveloping cells throughout the level of the narrow path (Fig. 3F) and are surrounded by the cuticular sheath, which is enclosed itself by one or more enveloping cells, near the cuticular pore (Fig. 3E). The margin of the cuticular pore is projected distally into a ridge, but does not form such cuticular components as known in hair sensilla, companiform sensilla etc. of arthropods (Fig. 3C, McIver, 1975).

DISCUSSION

The structure of the hair of CFO coincides well with that of a dendritic outer segment of an arthropod sensory cell which displays a ciliary structure (Altner and Prilinger, 1980). The absence of pore signature in the copepodid-V male of O. davisae suggests that the CFO functions only in adult male. From these facts the CFO is supposed to be a sensory organ closely related to mating behavior. Figure 1 shows that CFO is widespread within the genus Oithona including both the oceanic (types A and C) and inlet (type B) species (see also Nishida, 1981) except O. oculata and O. rigida. As the cilia are easily damaged by formaldehyde fixation, probably all the species with pore signature have the hairs protruding from each pore except O. simplex whose pores seem to be more or less rudimentary (Fig. 2D).

What kind of stimulus is related to the CFO? The structure of cilium is similar to that of arthropod mechanoreceptor in that it is nonbranched, terminating into a bundle of many microtubules and protruding into surrounding water as a slender hair (McIver, 1975). Similar structures have been

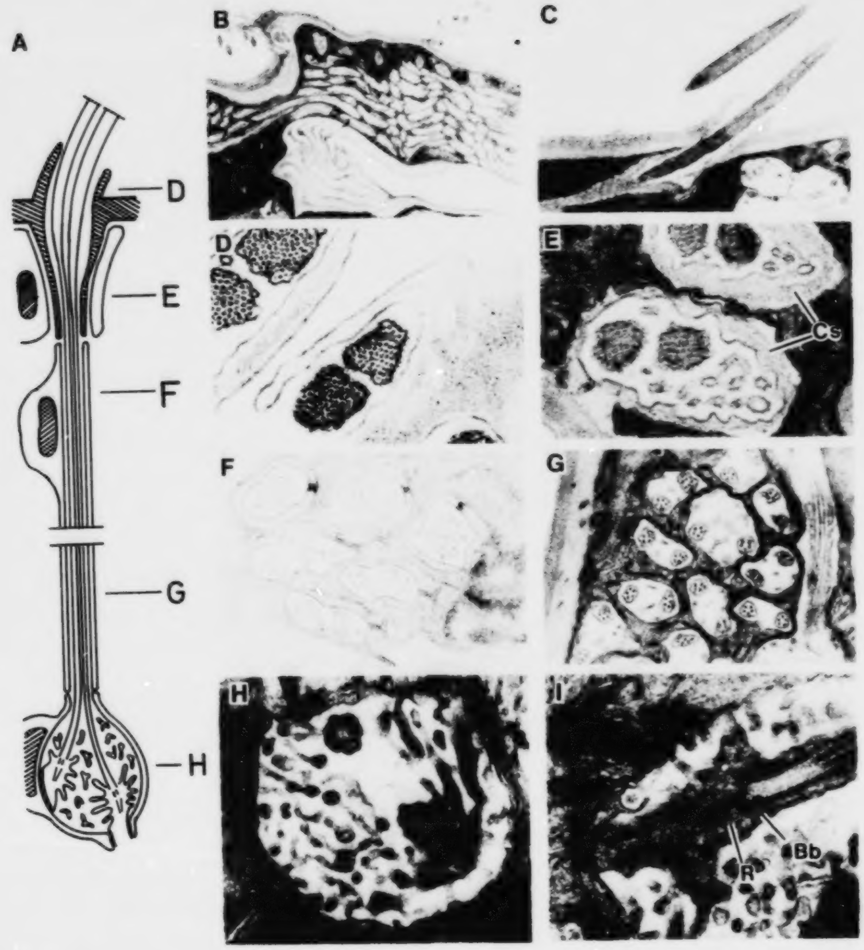


Figure 3. *Internal structure of the CFO of adult male* Oithona davisae. *A. Schematic drawing of the CFO. The letters D-H denote the levels of each sections shown in micrographs. B. Longitudinal section of cephalosome flap, x 3000. C. Longitudinal section of a cilium at the level of cuticular pore, x 8778. D-H. Cross sections of cilia at different levels showing decrease of number of microtubules basally; D-E, x 26000; F, x 20000; G, x 16000; H, x 20000. I. Semi-longitudinal section of the region of a basal body, x 26000. Bb, basal body; Cs, cuticular sheath; R, rootlet.*

reported in the first antenna of Cyclops (Strickler and Bal, 1973) and Diaptomus (Friedman, 1980). A marked difference of the CFO from these mechanoreceptors is the absence of the cuticular hair covering cilia. This condition permits the cilium to keep direct contact not only with chemical substance but also with mechanical stimuli such as vibration and flow of water. It is unlikely that the female could use the specialized setae of the fourth endopod for tactile interrogation of the male pore signature prior to spermatophore transfer (Ferrari and Bowman, 1980), because this movement would easily damage the hairs. There is no direct observation of the mating behavior of the oithonids except for the recent work by Uchima (personal communicaton) on O. davisae. He found that male O. davisae can seize female's fourth swimming legs with the first antennae without a preceding seizing of female's urosome or caudal setae as known in other copepods (Hill and Coker, 1930), and suggests the existence of a chemo- or mechanosensitive function in the pore signature to detect females effectively. On the other hand, the reduction of the fifth swimming legs and lack of specialized copulatory appendages in oithonids suggest that the CFO may function as a sensory organ in the process of spermatophore transfer to locate female's genital pore. But neither of these are conclusive yet. Future studies should include detailed observation of the mating behavior of oithonids and allied cyclopoids without CFO and electrophysiological experiments to obtain more direct evidence on the specificity of the sensory mechanism.

ACKNOWLEDGEMENTS

I thank Dr. F. D. Ferrari, Smithsonian Institution, who stimulated me to do this research. Thanks are also due to Dr. H. Ishikawa, Gumma Univ., and Dr. F. Yokohari, Fukuoka Univ., for their helpful comments and suggestions, and Ms. M. Hara, Ocean Research Institute, for her kind advice during the course of the electron microscopic observation.

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MORPHOLOGICAL COMPARISON OF THE MALE MOUTHPARTS OF HAPLOSTOMIDES WITH THOSE OF BOTRYLLOPHILUS

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Abstract: The male of Haplostomides (Cyclopoida, Ascidicolidae, Haplostominae) is reported from specimens collected from Ago Bay, Japan. The mouthparts of the male of Haplostomides are morphologically compared with those of the male of Botryllophilus, which belongs to the Botryllophilinae of the same family, from the same locality. The comparison supports the terminology used for the mouthparts of the Haplostominae from North America.

INTRODUCTION

The terminology used for the mouthparts of the Haplostominae from North America (Ooishi and Illg, 1977) was based on the results of studies (Ooishi, 1980) of their morphogenesis from the naupliar to the copepodid stage and the recognition of homologies in the adults in Haplostoma, Haplosaccus and Haplostomella, in which some mouthparts have been known to be lacking. It was emphasized (Ooishi, 1980) that studies on the mouthparts of the male of Haplostomides as well as similar studies on botryllophilins, which are the most closely related to haplostomins among the several groups of the Ascidicolidae, are needed to support the terminology used.

In studies of ascidicoles from the Pacific coastal waters of Japan, males of Haplostomides and Botryllophilus were fortunately found with their females from Ago Bay in central Japan. Before publishing the taxonomic study on these species, including the females, we present the morphology of the mouthparts of the males.

MATERIAL AND METHOD

Amaroucium sagamiense Tokioka, the host of the males of Haplostomides sp. and Botryllophilus sp., was obtained from oyster beds on January 9 and May 7, 1981.

The text-figures in this paper are based on several specimens in the lactic acid preparation for each species. The body length of a representative male for each species is 1.30 mm in Haplostomides sp. and 0.83 mm in Botryllophilus sp. measured from the anterior limit of the cephalosome to the end of the caudal rami, and the length including the caudal setae is 1.60 mm in Haplostomides sp. (Fig. 1a) and 1 mm in Botryllophilus sp. (Fig. 3a).

Abbreviations in the text-figures: A1, antennule; A2, antenna; MD, mandible; MX1, maxillule; MX2, maxilla; MXP, maxilliped.

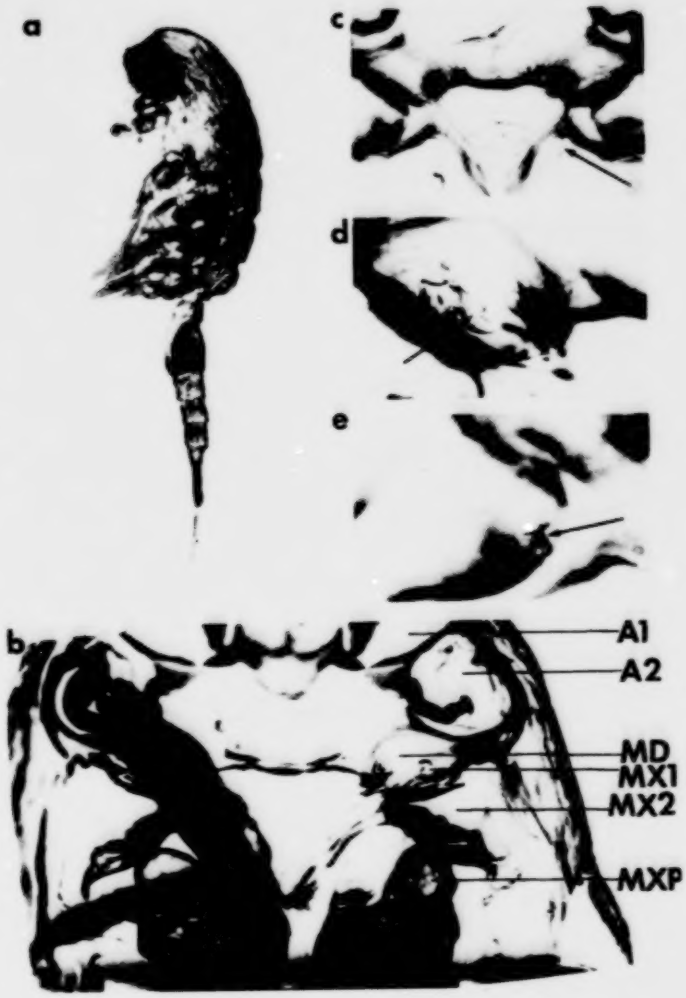


Figure 1. *Photomicrographs of Haplostomides sp., male, from Ago Bay:* **a**, *habitus, x65;* **b**, *cephalosome, showing arrangement of appendages, ventral, x480;* **c**, *oral area, arrow indicating setae of mandible, left, x350,* **d**, *oral area, arrow indicating maxillule, right, x720;* **e**, *oral area, arrow indicating setae of maxilla, right, x847.*

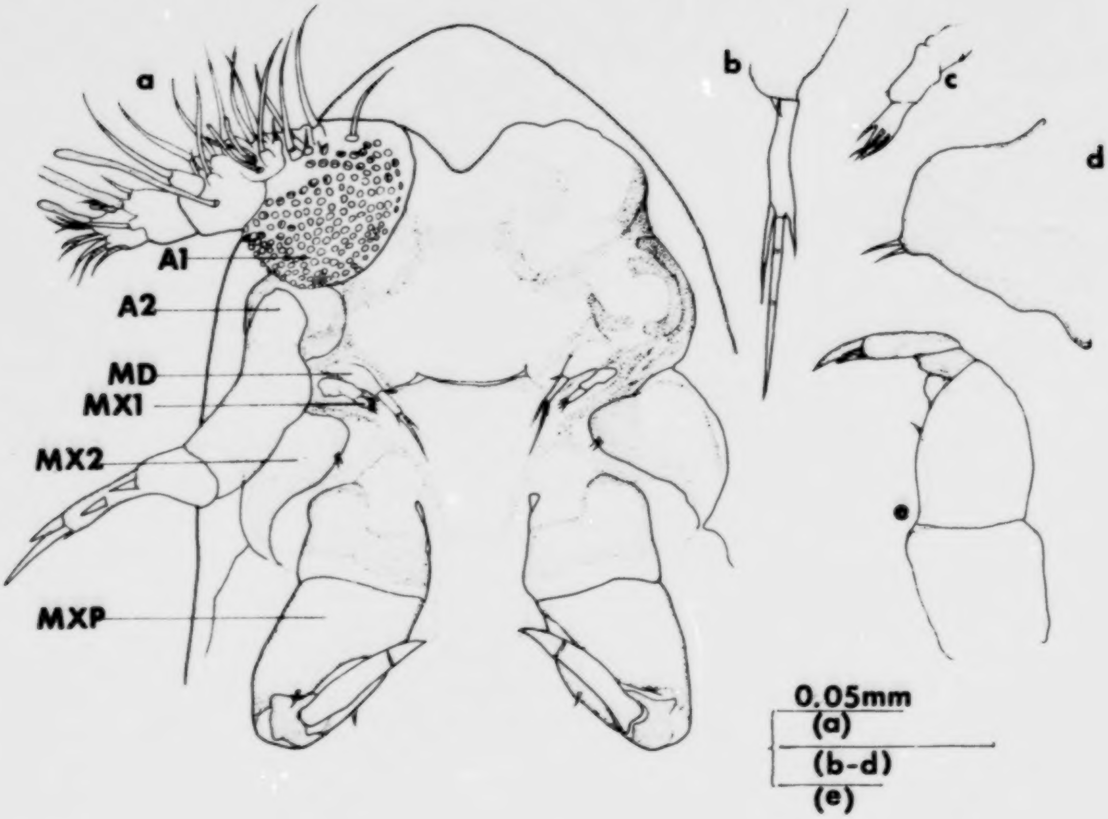

a
b
c
d
e
A1
A2
MD
MX1
MX2
MXP
0.05mm
(a)
(b-d)
(e)

Figure 2. Haplostomides sp., male, from Ago Bay: **a**, cephalosome, showing arrangement of appendages; **b**, mandible, left; **c**, maxillule, left; **d**, maxilla, left; **e**, maxilliped, left, posterior.

RESULTS

The mouthparts of the male of Haplostomides: The mouthparts consist of mandibles, maxillules, maxillae and maxillipeds (Figs. 1b, 2a). The mandible and maxillule are extremely small in comparison with the maxilla and maxilliped. All these mouthparts are arranged in relation to a pattern of sclerotization of the ventral surface of the head proper.

The mandible (Figs. 1c, 2a, b) has only 1 articulation. The proximal portion probably represents the protopodite protruding slightly from the body surface without articulation. The usual coxal lamella of the mandible is seemingly represented by a short stout seta protruding from the mediodistal corner of the protopodite. The distal article is cylindrical, about 6 times as long as wide, bearing 3 unequal setae, terminally, medially and laterally, around the apical margin.

The maxillule (Figs. 1d, 2a, c) is cylindrical, and weakly divided by an articulation at the distal third. The mediodistal corner of the proximal portion is ornamented with a few minute hairs. The distal article terminates in 4 subequal naked setae.

The maxilla (Figs. 1e, 2a, d) consists of a large subtriangular sack-like lobe protruding medially, bearing anteriorly and posteriorly 2 naked subequal short setae on the medially protruding apex.

In the maxilliped (Figs. 2a, e) the large basal segment is unarmed, the similarly large second segment tapers slightly and has 2 setules near the distal end on the medial margin. The smallest third segment is unarmed, and supports the terminal claw which is apparently divided into 2 articles at the distal third: the basal article with 1 setule near the anterior end and the distal article with 1 spinule-like element protruding from the medial base near the setule.

The mouthparts of the male of Botryllophilus: The arrangement and structure of the mouthparts of the male of Botryllophilus (Figs. 3b, 4a) are astonishingly similar to those of Haplostomides.

As in Haplostomides the mandible (Figs. 3c, 4a, b) is reduced relative to that of the female. All the elements of the armature are represented, but more developed in Botryllophilus in both structure and armature. The coxopodite retains a small but clearly demarcated gnathobasic portion which has never been recognized in males of Botryllophilus so far reported, including B. ruber Hesse, 1864 and unidentified species depicted by several previous authors. The uniramous distal article is an unsegmented, elongated cylindrical lobe about 2.4 times as long as the widest part of the distal third; the distal end reaches to about the basal third of the proximal segment of the maxilliped. The armature consists of 1 long plumose seta and 2 minute setules behind the seta midway on the lateral margin; 1 anterior, slender naked seta and 1 posterior, minute setule on the medial margin near the apex; and 3 graduated naked setae and 1 minute setule on the apical margin.

The maxillule (Figs. 3d, 4a, c) is much like that of Haplostomides in structure and armature with the exception of the number of setae. The ornamentation consists of 5 short naked setae: 1 seta (not present in Haplostomides) on the mediodistal corner of the basal article and 4 setae on the apex.

The maxilla (Figs. 3e, 4a, d) is comparable to that of Haplostomides, but more setiferous. The armature consists of 7 setae, including at least 2 plumose setae, arranged on the central portion of the medial margin.

The maxilliped (Figs. 4a, e) is substantially comparable to that of Haplostomides, but the armature differs by 1 medial setule midway on the large basal segment. There is 1 more setule at the distal third on the basal article of the terminal claw.

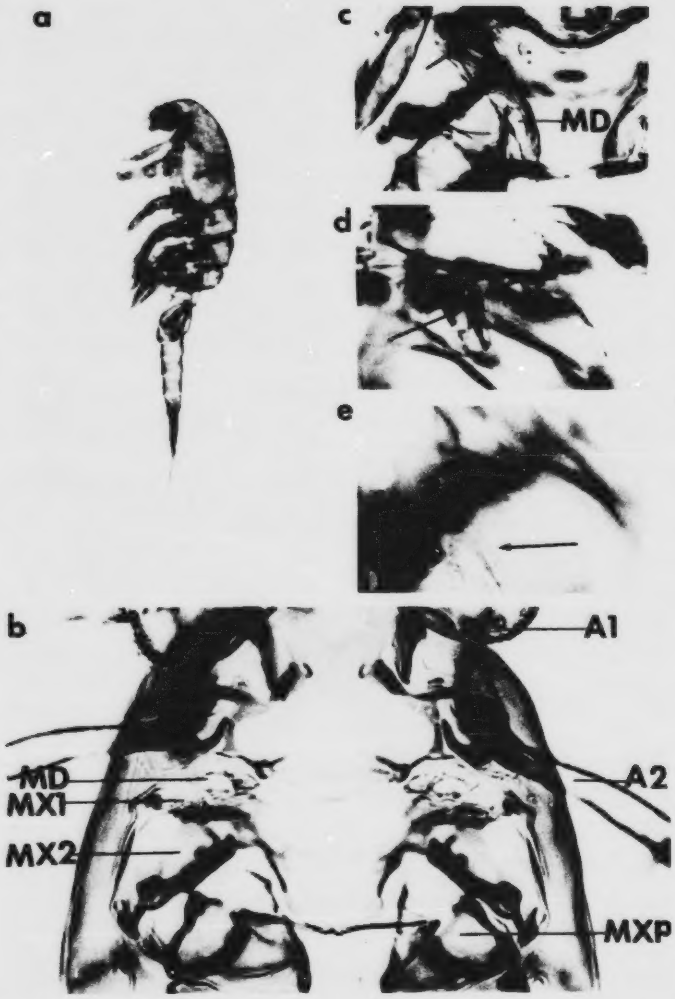
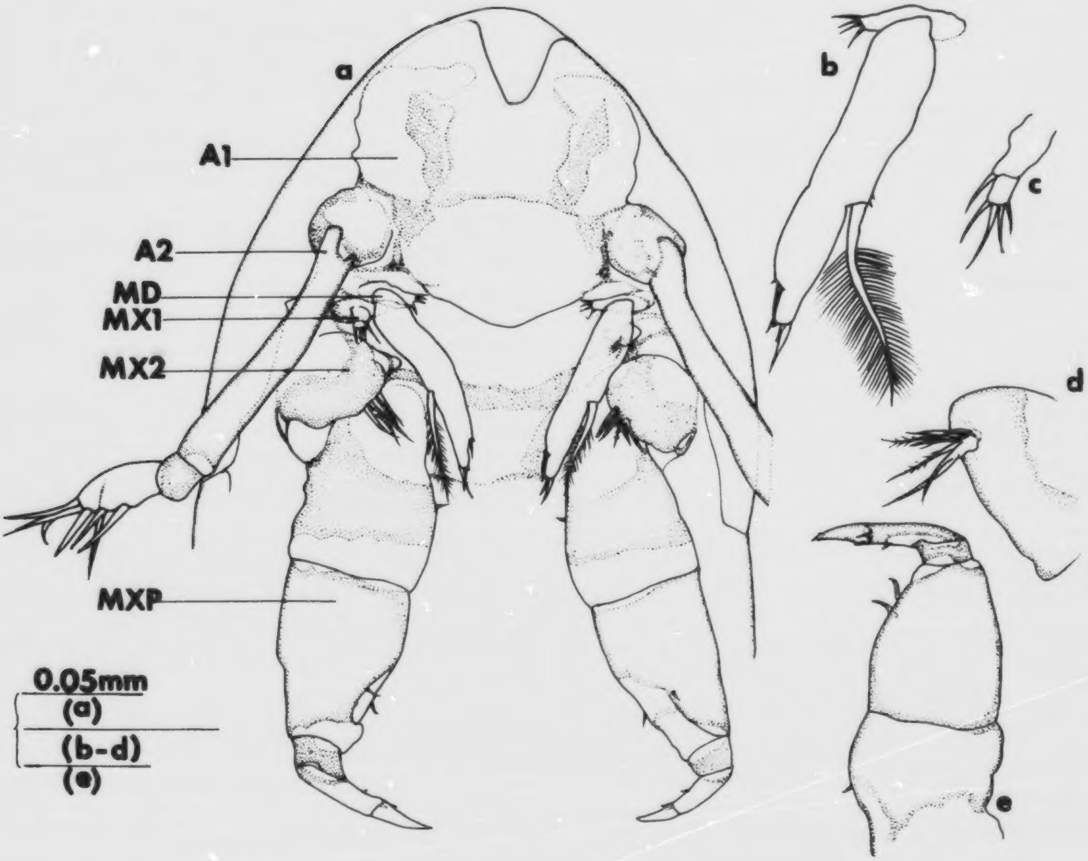


Figure 3. *Photomicrographs of* *Botryllophilus* *sp., male, from Ago Bay:* ***a**, habitus, x76;* ***b**, cephalosome, showing arrangement of appendages, ventral, x440;* ***c**, oral area, arrow indicating gnathobasic portion of mandible, right, x374;* ***d**, oral area, arrow indicating maxillule, right, x1077;* ***e**, oral area, arrow indicating setae of maxilla, right, x800.*


a
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A1
A2
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MX1
MX2
MXP
0.05mm
(a)
(b-d)
(e)

Figure 4. Botryllophilus sp., male, from Ago Bay: **a**, cephalosome, showing arrangement of appendages; **b**, mandible, left; **c**, maxillule, left; **d**, maxilla, left; **e**, maxilliped, left, posterior.

The terminology of the mouthparts of the Haplostominae: The arrangement of the male mouthparts of Haplostomides sp. from Ago Bay is the same as that of an unidentified male from North America, which we assumed (Ooishi and Illg, 1977, p. 78) to be a male of Haplostomides. Ooishi illustrated its mouthparts (1980, p. 284, Fig. 8). The mouthparts of these 2 males correspond generally in structure and ornamentation. In life the coloration of the male from Ago Bay is comparable to the unidentified male. Moreover, the female of Haplostomides sp. from Ago Bay bears a strong morphological resemblance to the female of Haplostomides luteolus from North America. We conclude, therefore, that the unidentified male (Ooishi and Illg, 1977) is the male of H. luteolus and the use of it as additional support (Ooishi, 1980, p. 283) for the terminology used for the mouthparts is reasonable.

DISCUSSION

Before the study on the Ascidicolidae by Illg and Dudley (1980), the male mouthparts of Botryllophilus had been considered as consisting of only 2 pairs: mandibles and maxillipeds (Schellenberg, 1922) for B. ruber Hesse, 1864; mandibles and 2nd maxillipeds (Bresciani and Lützen, 1962) for B. ruber; mandibles and 2nd maxillae, for B. sp. described and figured as the male of Haplostoma brevicauda by Canu, 1892, but, as pointed out by Schellenberg (1922), actually the male of Botryllophilus. In the study of the male of Botryllophilus sp. from North America by Illg and Dudley (1980), however, the specimen is seen as possessing 4 pairs of mouthparts including a much modified mandible lacking masticatory lamella; the maxillule and maxilla, reduced to minute vestiges; and a large clawed maxilliped. The arrangement of the mouthparts of the male Botryllophilus sp. from North America is like that of the mouthparts of the male Botryllophilus from Ago Bay.

The present paper is the first in which the male mouthparts of Haplostomides and Botryllophilus are described and compared. The findings support the terminology used by us for the mouthparts in descriptions of species in the subfamily Haplostominae, family Ascidicolidae, from the Northeastern Pacific, and in discussions of the comparative morphology of the reductions of the mouthparts through the family Ascidicolidae. The positions of the mouthparts found here confirm our basis for interpreting the presence or absence of specific appendages in the genera with reduced mouthpart complements (Ooishi, 1980, pp. 283-285).

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THE GEOGRAPHICAL DISTRIBUTION OF MESOCYCLOPS EDAX (S.A. FORBES) IN LAKES OF CANADA

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Abstract: Mid-summer samples were taken in 700 lakes distributed throughout Canada from 55° to 140°W longitude and from 41° to 75° of N latitude.

The occurrence of Mesocyclops edax in Canada was found to be restricted to the eastern and central parts of the country - from Nova Scotia to Alberta. 61° N latitude appears to be the northern limit. Mesocyclops edax was found in a wide range of lakes sizes and depths, from very small to great lakes, often as a dominant cyclopoid.

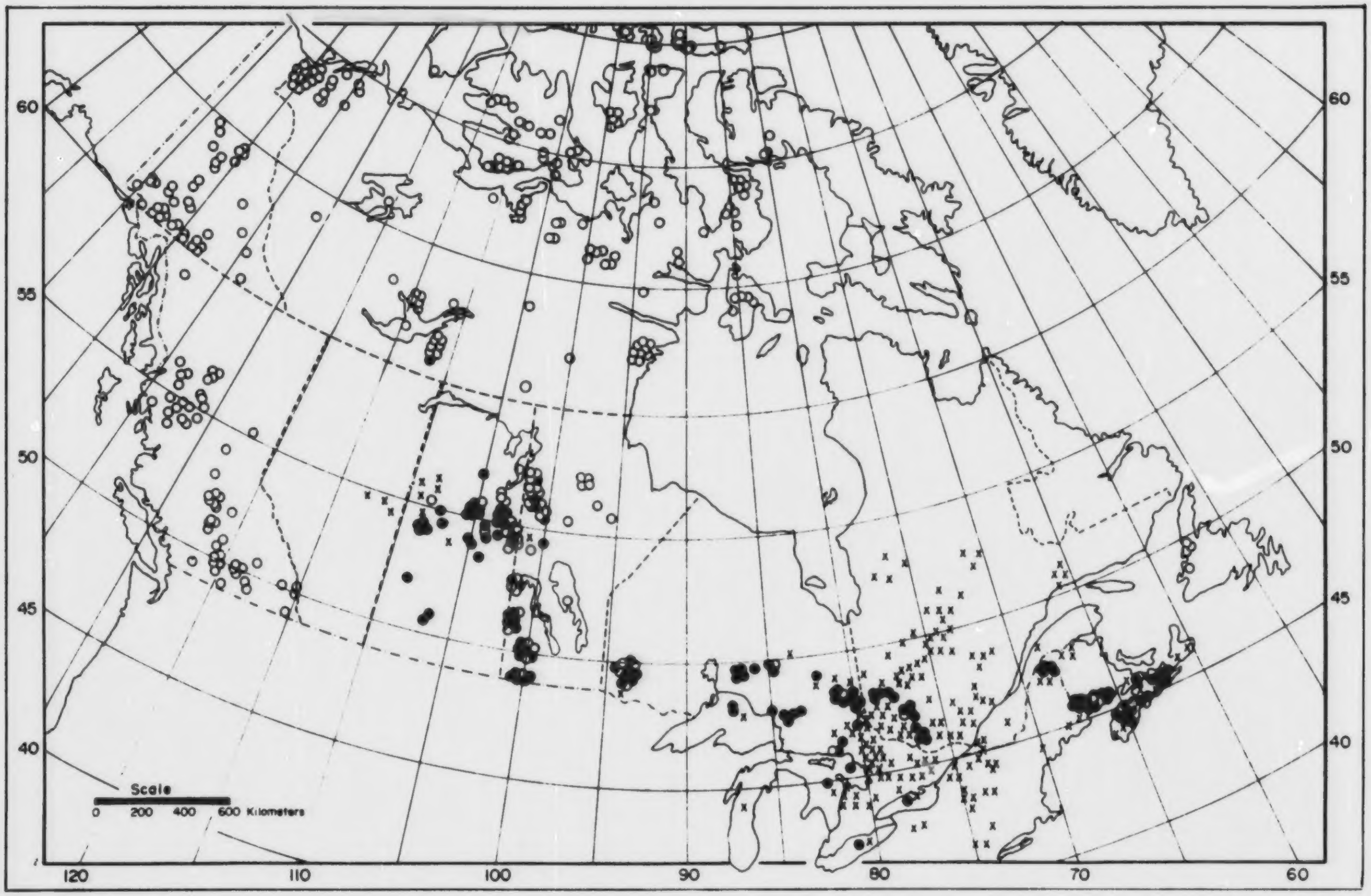
The frequency of occurrence of Mesocyclops edax was declining towards the northern margins of its distribution area and was well correlated with the duration of the ice-free period and mean July air temperature.

A hypothesis has been discussed that populations of this species which inhabit the margins of its distribution area are more vulnerable to antropogenic environmental stresses than the centrally located populations.

The knowledge of the distribution of planktonic copepods in Canada is rather limited. There are numerous records of occurrences of various species in particular parts of the country (e.g. Carl, 1940; Reed, 1964; Dadswell, 1974; Anderson, 1974; Smith and Fernando, 1977; Carter et al., 1980), as well as some more general remarks on the distribution in identification keys (Yeatman, 1959; Wilson and Yeatman in Ward and Whipple, 1959), however, no comprehensive monograph has been published which could include all of Canada.

Mesocyclops edax (S.A. Forbes), one of the most widely distributed copepod species, was originally described as Cyclops edax by S.A. Forbes in 1891, later revised by E.B. Forbes in 1897. Marsh (1910) did not recognize the differences between C. edax and the relatively rare Cyclops leuckarti that E.B. Forbes had adduced and concluded that none of the differences were of more than varietal value. Also Kiefer (1929) listed the species as Mesocyclops leuckarti edax E.B. Forbes. The thorough review by Coker (1943) led him to recognize Mesocyclops edax (S.A. Forbes) as a clearly distinct species. Yeatman (1959), who contributed substantially to Coker's (1943) review, confirmed the distinct character of the species in the second edition of Ward and Whipple Fresh-water Biology, edited by W.T. Edmondson (1959). Until that time, literature references on the species could be found under that least seven names: Cyclops leuckarti Claus, Mesocyclops leuckarti (Claus), Cyclops obsoletus (Koch), Mesocyclops obsoletus Sars, Cyclops leeuwenhoekii Hoek, Cyclops edax S.A. Forbes, Mesocyclops edax (S.A. Forbes).

It is particularly difficult to decide which of the older references relate to the real Mesocyclops leuckarti (Claus), and which one is used as a synonym of Mesocyclops edax E.B. Forbes. For these reasons the literature records on Mesocyclops edax distribution in Canada are treated, in this paper, separately from original data and verified identifications.


60
55
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0 200 400 600 Kilometers

Figure 1. *The distribution of Mesocyclops edax (S.A. Forbes) in lakes of Canada. Open and full circles - the distribution of lakes sampled. Full circles - lakes with Mesocyclops edax. Crosses - literature records of Mesocyclops edax. The density of symbols is slightly reduced in areas of high sampling density.*

METHODS

Collections have been made in more than 700 lakes in all major regions of Canada for many years, starting from 1961 until 1983. Lakes of a wide range of sizes (from 0.01-82,000 km²), depths (from 1-614 m) and latitudes (42°-76°) were sampled (Fig. 1). Samples were taken in mid-summer, mostly in August, ranging from July to September in the central part of the lake. A 77 µm mesh size Wisconsin plankton net 20 cm mouth diameter was used in a vertical haul from near bottom to the surface. Samples were preserved in 4% formaldehyde.

RESULTS

Of the 700 lakes samples, M. edax was identified or verified in 272 lakes (Fig. 1). They were located in Nova Scotia, New Brunswick, Quebec, Ontario, Manitoba, Saskatchewan and the Northwest Territories. In spite of intensive sampling, the species was not found in lakes within and west of the Rocky Mountains (British Columbia and Yukon) and in most of the Northwest Territories. In central Canada, M. edax occurred up to 61° and in eastern Canada up to 54°N latitude. The limited number of samples from Albertan lakes does not allow a precise definition of the western extend of the species.

In addition to these data, some verified literature records of the occurrence of M. edax have been included on the map. Integrated with my findings (Fig. 1), they provide a more complete pattern of distribution. They confirm that none of the literature records west of central Alberta lists M. edax. A very extensive and thorough study by Anderson (1974) did not reveal this species in any of the 340 lakes and ponds in the Rocky Mountains. There are few records from Alberta (Prepas and Vickers, 1984) and from Saskatchewan (Rawson, 1960 and Reed, 1964). Only in a few lakes east of James Bay was this species found in spite of extensive sampling in this area by Pinnel-Alloul et al.(1979). A high frequency of occurrence in southern Ontario, south Quebec and Nova Scotia lakes confirmed the findings by Carter et al. (1980). None of the available records have shown M. edax in lakes of Newfoundland.

In one of the most thoroughly studied, chemically homogeneous group of lakes in northwestern Ontario, M. edax was recorded from lakes of a wide range of surface area, depth and water transparency. However, it was found to be more abundant (> 10% of the total crustacean number) only in smaller, shallower lakes of low to medium transparency (Patalas, 1971; Fig. 2). This general pattern seems to be characteristic for most of the northwestern and southern Ontario, Nova Scotia and New Brunswick lakes. The species was never abundant in deeper and more transparent lakes. Its occurrence in the Laurentian Great Lakes confirms this pattern. Although present in all five lakes (Erie, Ontario, Huron, Superior and Michigan), it was found to be relatively abundant (2.2-10.8%) only in Lake Erie, the shallowest and least transparent of them (Patalas, 1969, 1975). In the remaining Great Lakes, M. edax was encountered very rarely and only in the nearshore zone. A similar pattern prevailed in Lake Winnipeg with M. edax being found only in the areas adjacent to river inlets (Patalas, 1981) and Southern Indian Lake, where this species was found only in embayments with temperature a few degrees higher than in the open waters (Patalas and Salki, 1984).

The area of occurrence of M. edax as shown in Fig. 1, illustrates only one aspect of the distribution. The other, perhaps a more interesting aspect, is the frequency with which the species was found in different groups of lakes within the distribution area (Fig. 3). Ninety to 96% of the lakes in southern Ontario, New Brunswick and Nova Scotia were inhabited by M. edax. The frequency of its

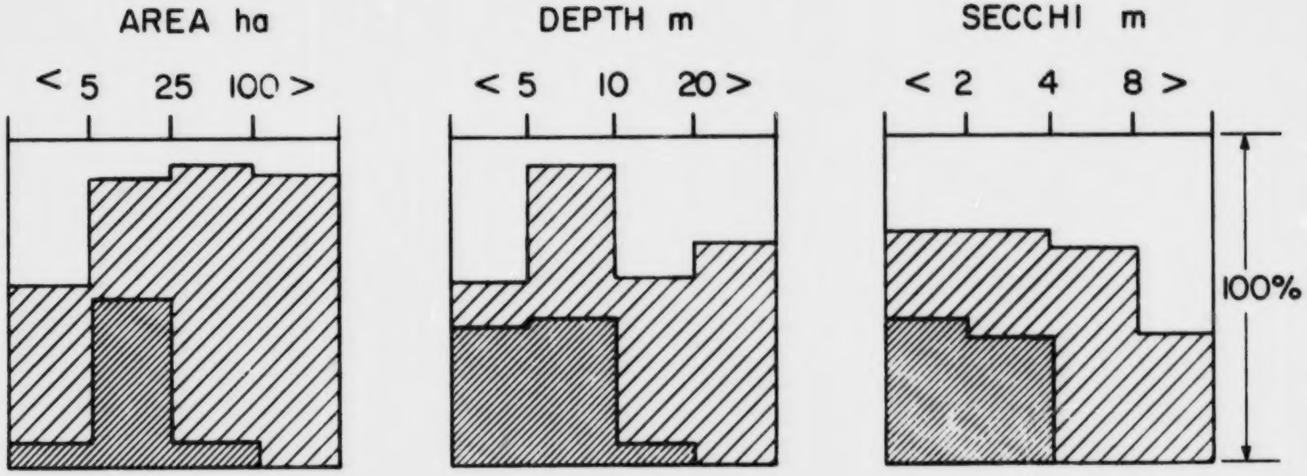
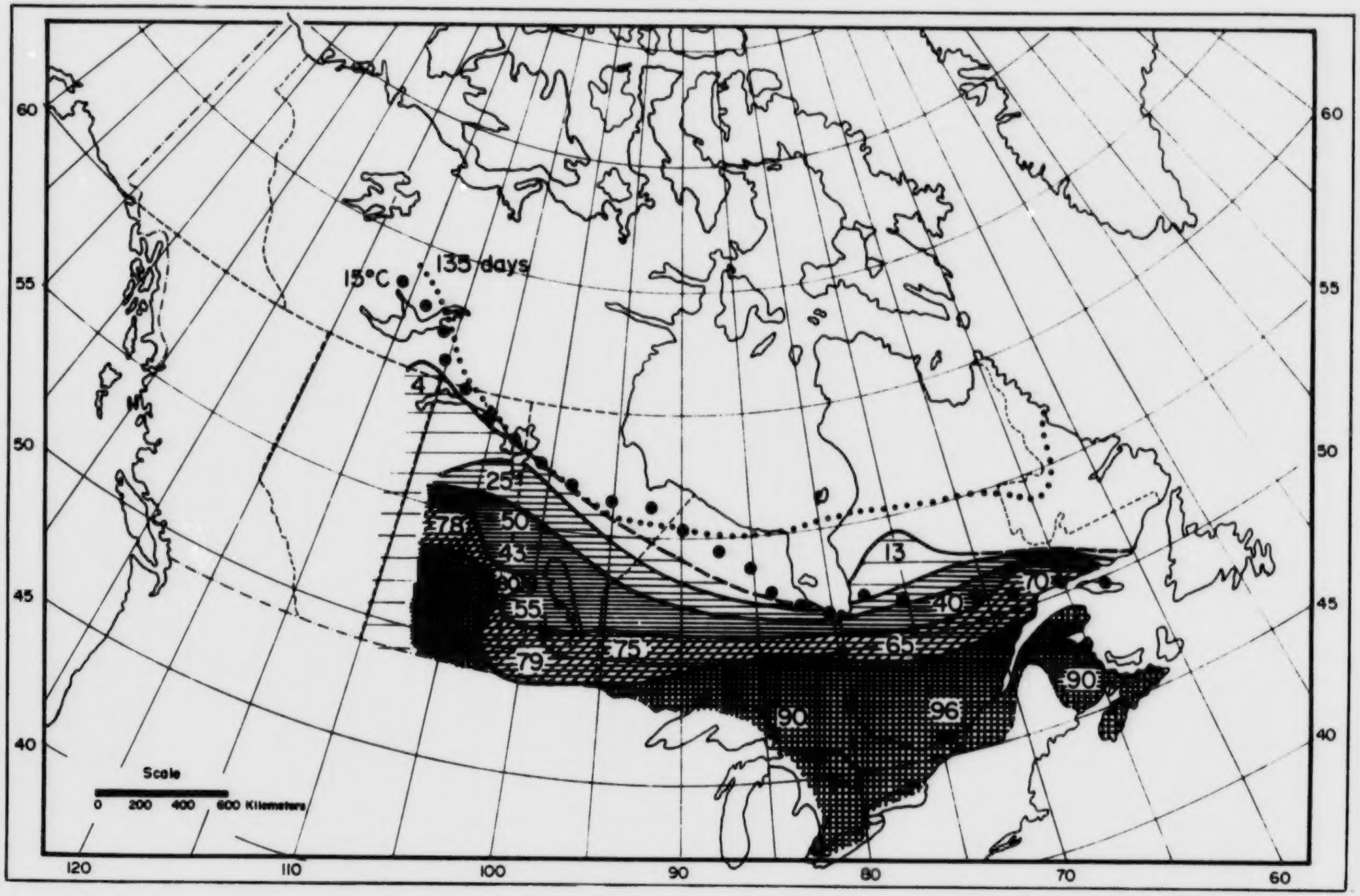


Figure 2. *Frequency distribution of Mesocyclops edax in ELA lakes (northwestern Ontario) of different area, depth and water transparency. The shaded part of the bar refers to the percentage of lakes in which the species occurred. The height of the darker bar indicates the percentage of lakes in which the species was dominant (accounted for more than 10% of all crustaceans).*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96
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120
110
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70
60

Figure 3. *The extent of the area inhabited by* *__Mesocyclops__ __edax__* *and the percentage of occurrence of the species in various groups of lakes across Canada. The dotted lines indicate the mean daily July air temperature (large dots) and the duration of the ice-free period (according to Hydrological Atlas of Canada).*

occurrence declined to 75% in northwestern Ontario (ELA). In Manitoba the percentage of lakes with M. edax shows a declining trend from 79% in the south (49°) to 25% in the Lynn Lake area (57°N latitude). Only in 4% of the lakes was the species found in its most northerly location - south of Great Slave Lake and in 13% of lakes in central Quebec, east of James Bay. In all these areas, close to the northern border of the distribution, M. edax was found always in small numbers, mostly below 1% and never exceeding 10% of the total crustacean abundance.

DISCUSSION

There are two main reasons why planktonic organisms may occur in a specific locality:

a) they must have had an opportunity in the past to be dispersed into the area;

b) they were able to survive the existing physical, chemical and biological environment.

The main area of the distribution of M. edax (S.A. Forbes) is North America. It is not known outside of the Nearctic. Coker (1943) considers it as "probably our most common limnetic cyclopoid". Also Yeatman (1959) and Pennak (1978) describe it as "common, widespread limnetic species". Coker (1943) reports this species from New York, Oklahoma, North Carolina, Mexico, and Massachussetts. Patalas (1964) found it in lakes of the Colorado plains. In spite of an extensive literature search, no records of occurrence were found in U.S.A. west of the Rocky Mountains, which appears to be an efficient geographical barrier for this species throughout the entire North American continent.

The distribution of this species in Canada outlines the northern extend of the area. With the warming of the climate and retreat of the Laurentide ice sheet, M. edax dispersed from the central and eastern regions of the North American continent, northward, reaching a latitude of 54° and 61° in eastern and central Canada respectively. Geology of the drainage basin does not seem to play an important role. M. edax occurs within and outside of the Precambrian Shield in the praire - sedimentary basin. It was found in lakes with total dissolved solids up to 1500 $mg.L^{-1}$ but was absent in lakes with TDS higher than that.

M. edax belongs to a genus in which the species are largely tropical (Gurney, 1933). One could then expect that the northern extent of the species would be limited by some climatic factors.

Two factors have been considered:

a) the daily mean July air temperature, and related lake water temperature,

b) the duration of the ice-free season.

The northern extent of the species is well-defined by the isotherm 15°C of the daily mean temperature in July (Fig. 3). The lake water epilimnetic temperature, particularly in smaller lakes, follows the mean daily air temperature closely. With the July average 15°C, the lakes' temperature in epilimnion can reach up to 20°C at the end of July and beginning of August.

The mean duration of the ice-free period at the northern extent of M. edax distribution is limited to about 135 days (1-15 June to 1 November, Anonymous, 1978). The frequency of occurrence of M. edax was conspicuously declining towards the margins of its distribution area.

A relationship between the frequency of occurrence, the mean July temperature and the duration of the ice-free period was tested. A linear correlation between the frequency of occurrence and temperature alone (Fig. 4) has shown a rather poor correlation coefficient $R^2 = 0.40$ (16 df). A better

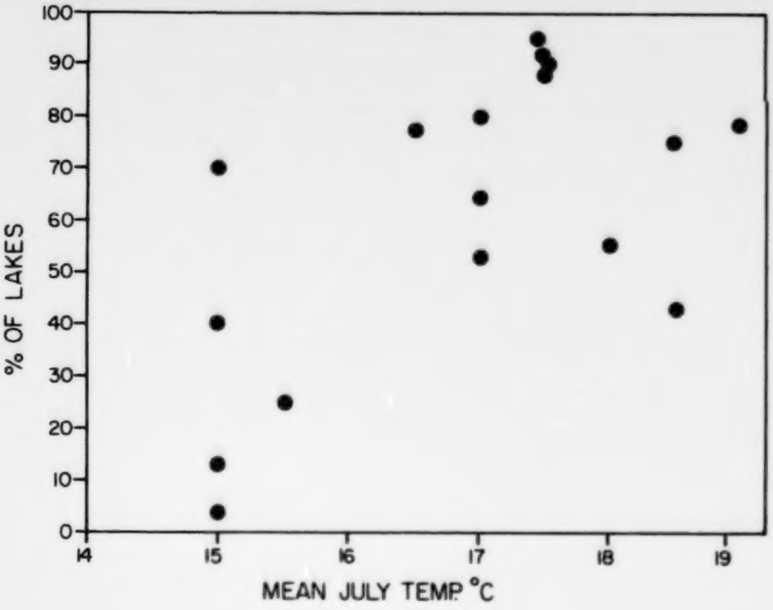

Figure 4. *The percentage of occurrence of* Mesocyclops edax *in various groups of lakes vs mean daily July air temperature.*

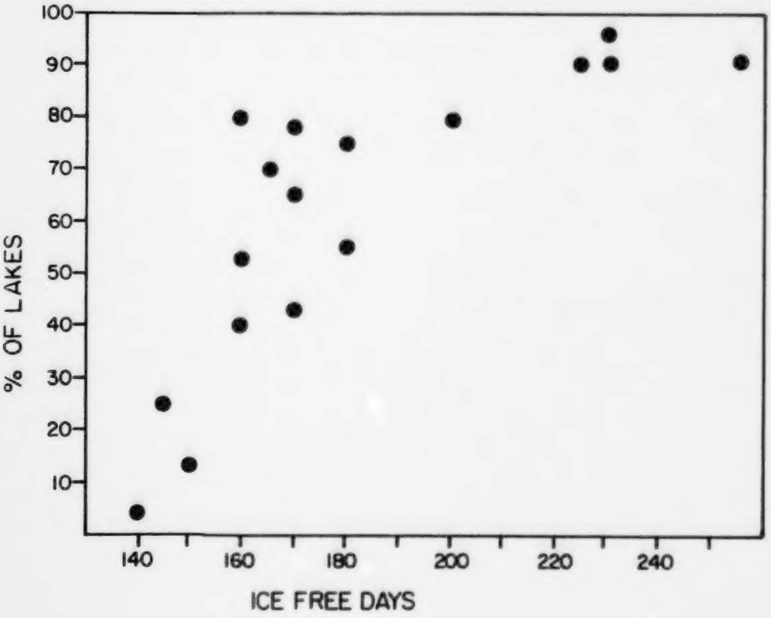

Figure 5. *The percentage of occurrence of* Mesocyclops edax *in various groups of lakes vs the duration of the ice-free period.*

correlation existed between the M. edax frequency of occurrence and the ice-free season (Fig. 5) with $R^2 = 0.65$. In areas with the ice-free season shorter than 200 days, the number of lakes inhabited by M. edax was reduced gradually to a complete disappearance with the ice-free season shorter than 140 days. These two parameters are apparently mutually dependent and an interaction could be expected. Hence, the first order - interactive multiple regression analysis was carried out using temperature, ice-free days and their interaction term. They were all highly significant at $p > 0.99$, $R^2 = 0.825$ (3, 13 df).

In conclusion, mid-summer temperature and ice-free season length not only apparently define the northern extent of M. edax, but they may also determine the diminishing relative frequency of lakes inhabited by this species as the northern boundary of distribution is approached. One could hypothesize on the basis of these findings that populations of this species which inhabit the margins of its distribution area are exposed to more rigid physical environmental stress than populations in the centre of the distribution. These populations might be more vulnerable to additional environmental stresses, in which case environmental anthropogenic impact (eutrophication, acidification, toxic substances, etc.) could have more severe effect on these marginal populations than on centrally located ones.

This hypothesis, if proven correct, would have far reaching consequences in interpreting and predicting the environmental impact on living organisms as a gradation of population responses would be expected rather than a single fixed response.

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DISTRIBUTION DE TAILLE D'UNE ESPECE DE COPEPODE EN RELATION AVEC SA DISTRIBUTION SPATIALE

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Laboratoire Arago, 66650 Banyuls-sur-mer, France

Abstract: Plankton sampling carried out during two cruises in the eastern part of the English Channel provided Temora longicornis for a population study. T. longicornis is more abundant near the coast than offshore (46% and about 10% of all the copepods respectively).
The frequency distribution of T. longicornis size (in terms of body length) shows that size increases gradually from inshore to offshore.

The size spectrum in adults appears to be plurimodal, 4 to 5 size classes can be defined in each sample. Minimum and maximum values are related by a multiplying factor lying between 1.4 and 2 both for males and females. Short term (8 days) and long term (one year) replication samples have confirmed this tendency.

INTRODUCTION

L'étude des dimension chez les Copépodes planctoniques, fournit des informations sur la structure de la population. Les caractéristiques biométriques traduisent dans une certaine mesure les conditions régnant lors de la croissance qu'il s'agisse de la température (McLaren, 1965; Durbin et Durbin, 1978) et probablement de la nourriture disponible, ainsi que l'ont montré des élevages au laboratoire (Durbin et al., 1983). Elles permettent de séparer dans un même prélèvement des individus appartenant à des cohortes ou des générations différentes (McLaren, 1978), ou d'origine étrangère, amenées dans la communauté étudiée par des mouvements hydrodynamiques (Mullin, 1969).

En Mer du Nord et en Manche, les variations de taille de populations locales liées aux variations saisonnières de température ont été mises en évidence pour différentes espèces (Adler et Jespersen, 1920; Digby, 1950; Marshall, 1949; Razouls, 1965; Brylinski, 1979; Le Fevre-Lehocrff et Quintin, 1979).

Le problème de la variation de taille pour une saison donnée en différents points d'un secteur géographique est par contre peu étudié, bien que l'on ait souvent signalé dans un prélèvement l'existence de grandes et petites formes dans une même espèce (Mullin, 1969).

L'examen des population de Temora longicornis lors d'une campagne en Manche orientale a révélé l'hétérogénéité spatiale des adultes selon des critères de taille, ce qui est tout à fait concordant avec les disparités de taille des T. longicornis observées par Evans (1981) en Mer du Nord.

La campagne ECOMANCHE avait pour but la description du système pélagique dans la partie orientale de la Manche, la mise en évidence de ses caractéristiques et de leur variabilité en rapport avec la distribution spatiale, et l'évolution du système à moyen et long terme (Boucher, 1980).

La répétition du même quadrillage à huit jours d'intervalle, et l'année suivante permet des comparaisons avec un état de référence choisi au moment du "bloom" de printemps.

MATERIEL ET METHODES

Les Copépodes étudiés proviennent des prélèvements zooplanctoniques des campagnes ECOMANCHE I: premier passage (12-21-V-1978), deuxième passage (22-24-V-1978) et ECOMANCHE II (12-22-V-1979).

La répartition géographique des Temora longicornis adultes ♀ et ♂ selon leur taille a été suivie en cinq points du quadrillage de l'ensemble du bassin oriental de la Manche (Fig. 1).

Ces stations on été choisies en fonction de leur situation particulière dans la zone étudiée, de la côte vers le large: les stations 21(1) (ƒ: 49°38' N - G: 0°05' W) et 33 (ƒ: 59°48' N - G: 1°21' E) sont les plus côtières; les stations 19 (ƒ: 50°03' N - G: 0°13' W), 39 (ƒ: 50°19' N - G: 0°59' W) sont réparties vers le large, la station 91 (ƒ: 50°33' N - G: 0°29' W) se rapprochant des côtes anglaises.

Les pêches de zooplancton ont été faites par des traits verticaux du fond à la surface avec un filet WP2 (200 µm de vide de maille).

Après dénombrement des Temora longicornis de 30 à 100 animaux adultes de chaques sexe ont été prévelés au hasard et mesurés dorsalement de l'extrémité frontale, au milieu du bord postérieur du dernier segment thoracique.

La distribution spectrale des classes de taille a été établie en utilisant un découpage entre les longueurs minimales et maximales absolues pour l'ensemble des pêches étudiées, le nombre de classes, K, dans cet intervalle étant déterminé par: $K = 5 \log_{10} N$, où N = nombre d'individus mesurés, (Caillez et Pages, 1976).

Les données on été traitées par une analyse de correspondance en collaboration avec F. De Bovée.

RESULTATS

1) Evolution des longueurs du céphalothorax

D'une manière générale, on observe que les longueurs moyennes du céphalothorax des T. longicornis ♀ et ♂ croissent des station côtières vers celles du large à quelques variantes près dans la forme de la courbe, selon la grille considérée (Fig. 2). Cette évolution est confirmée par l'analyse des correspondances entre classe de taille et stations.

Pour les femelles, les valeurs moyennes se situent entre 1027 µm et 1228 (premier passage), 982 et 1167 µm (deuxième passage), 938 et 1133 µm (troisième passage).

Les longueurs de mâles, suivent une évolution parallèle tout en demeurant toujours inférieures à celles des femelles. Les valeurs s'échelonnent de 914 à 1068 µm et 861 à 1002 µm pour chacun des trois passage respectivement.

La variabilité des mesures, exprimée par le coefficient de variation est de l'ordre de 8 à 13% chez les femelles et légèrement plus faible (5 à 10%) chez les mâles, sans disparité notable de ces coefficients entre les différentes grilles de passage (Tableau 1).

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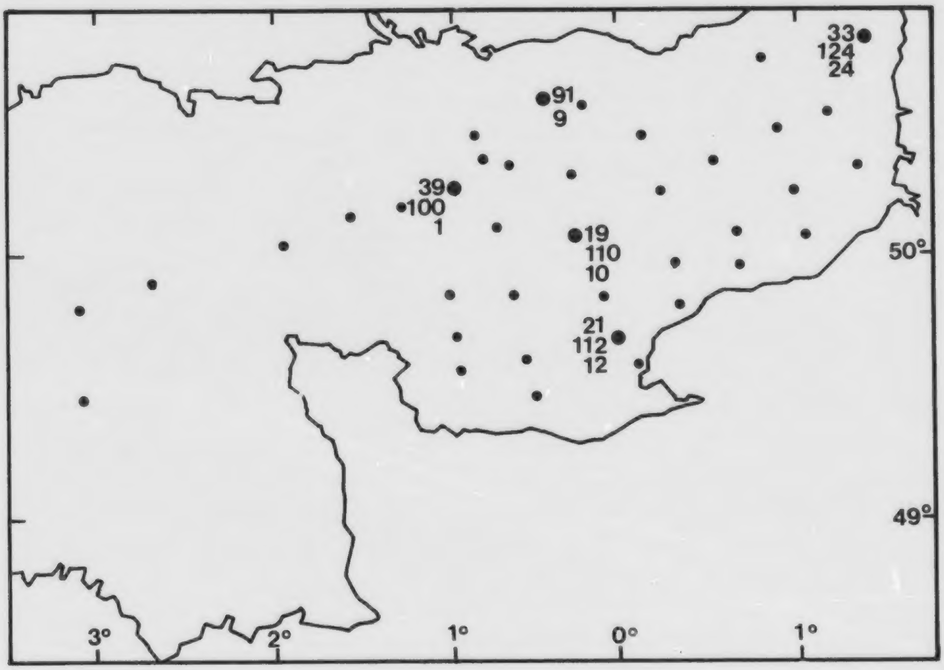
(1) référence au n° de la station du premier passage d'ECOMANCHE I. Les n° des stations homologues des deux autres passages sont portés sur la Fig. 1.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0°
1°

Figure 1. *Localisation des stations au cours des campagnes ECOMANCHE I (1er passage: 14-20-V-78 - 2ème passage: 22-23-V-78). ECOMANCHE II (3ème passage: 13-15-VI-79) en Manche Orientale.*

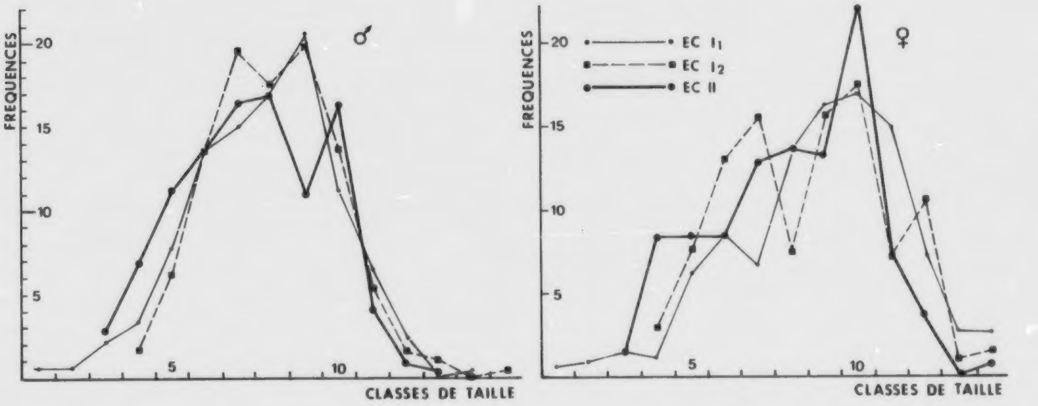

Figure 3. *Fréquence de distribution des classes de tailles du céphalothorax pour l'ensemble des stations de chaque grille. ECI$_1$: 1ère grille; ECI$_2$: 2ème grille; ECII: 3ème grille.*

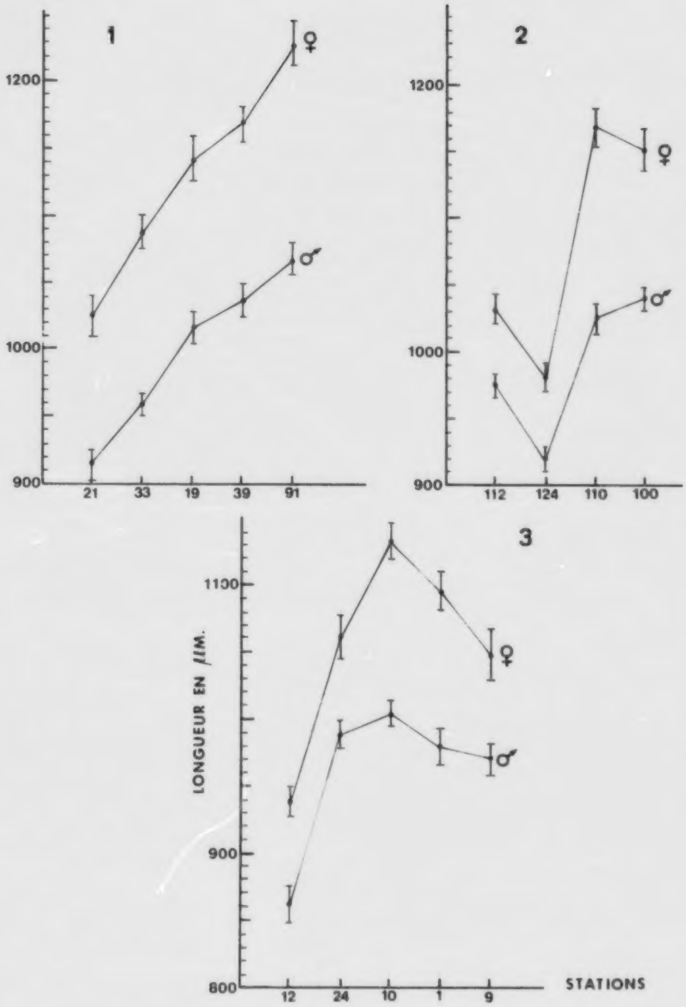

Figure 2. *Longueurs moyennes du céphalothorax de Temora longicornis ♀ et ♂ (barres verticales: ± Erreur standard).1 = 1er passage; 2 = 2ème passage; 3 = 3ème passage.*

Tableau 1: *Longueur du céphalothorax de Temora longicornis durant la campagne ECOMANCHE I et II. Taille moyenne en µm; ES = Erreur standard; CV % = coefficient de variation. (n = 50 sauf autre indication).* ECI_1 *= 14-20-V-78;* ECI_2 *= 22-23-V-78; ECII = 13-15-VI-79.*

Stations	Femelles		CV %	Males		CV %
	Moyenne + E.S.	Limites		Moyenne + E.S.	Limites	
21	1027 ± 13,5	660 - 1298	13,2	914 ± 9,7	649 - 1138	10,6
	(n = 100)			(n = 100)		
33	1085 ± 12,0	755 - 1394	11,1	959 ± 7,50	766 - 1138	7,8
	(n = 100)			(n = 100)		
19	1142 ± 17,0	819 - 1393	10,5	1017 ± 10,9	819 - 1244	7,6
ECI$_1$ 39	1169 ± 13,2	957 - 1351	8,0	1038 ± 11,08	830 - 1181	7,5
91	1228 ± 17,7	1021 - 1382	7,9	1068 ± 10,52	983 - 1148	5,4
	(n = 30)			(n = 30)		
112	1032 ± 13,8	832 - 1184	9,5	974 ± 9,3	832 - 1088	6,8
124	982 ± 10,5	864 - 1184	7,6	920 ± 8,7	832 - 1088	6,7
ECI$_2$ 110	1167 ± 13,6	880 - 1344	8,2	1024 ± 12,1	928 - 1280	9,4
100	1152 ± 15,4	864 - 1392	9,4	1040 ± 8,07	880 - 1152	5,5
-	-	-	-	-	-	-
12	938 ± 10,5	800 - 1072	7,9	861 ± 9,9	768 - 1056	8,2
24	1061 ± 16,3	800 - 1344	10,9	988 ± 9,7	848 - 1216	6,9
ECII 10	1133 ± 13,9	896 + 1344	8,7	1002 ± 12,6	800 - 1120	8,9
1	1096 ± 12,7	864 - 1248	8,1	980 ± 12,3	800 - 1152	8,7
9	1049 ± 18,9	832 - 1232	12,7	971 ± 12,2	768 - 1120	8,9

Pour chaque station l'accroissement maximal des tailles a été déterminé par la rapport, Ac, tel que Ac = Longueur minimale/Longueur maximale. Ces facteurs d'accroissement se situent entre 0.50 et 0.74 pour le premier passage où ils sont les plus importants. Ils sont légèrement inférieurs pour les deux autres passages: 0.59 à 0.75.

Pour les mâles, les accroissements pour le premier passage sont de 0.57 à 0.86 et pour les suivants de 0.68 à 0.76. A l'exception des 2 stations côtières d'ECI$_1$ les valeurs de Ac témoignent d'un étalement comparable de la gamme des tailles dans la zone étudiée.

Les valeurs moyennes des longueurs comparées entre les différentes stations pour chaque grille (test "t") indiquent en général une différence significative entre les stations de proche en proche de la côte vers le large, à l'exception des 2 stations du large (st. 19, 39, 100 et 110). Au cours des deux premiers passages (ECI$_1$ et ECI$_2$) séparés de 8 jours, les tailles moyenne des T. longicornis ♂ et ♀ sont comparables (différence non significative) à l'exception des individus de la station côtière la plus orientale (st. 124) nettement plus petits (982 µm) que ceux de la station homologue st. 33 (1085 µm).

Pour les station du troisième passage un mois plus tard (et à un an d'écart) (EC II), les longueurs moyennes aux cinq stations sont bien significativement différentes entre elles de proche en proche et l'on observe la même augmentation des longueurs des points côtiers vers ceux du large mais une différence non significative entre la station côtière la plus orientale (st. 24) et les station du large souligne l'existence d'un rapport entre ces trois points.

La question qui se pose est de savoir si l'on peut caractériser pour l'ensemble des station une seule population ou s'il existe plusieurs populations d'origine exogène?

2) Distribution selon les classes de taille des T. longicornis sauvages

Le calcul de l'intervalle des classes de taille effectué sur l'ensemble des mesures des trois passages donne le découpage suivant: pour les femelles, 14 classes de taille d'intervalle 52.5 µm (entre les valeurs extrèmes de longueur de 660 et 1395 µm). Get intervalle correspond à celui trouvé par Razouls et Guinness (1973) pour Temora stylifera, basé sur les écarts des longueurs moyennes des classes dominantes par pêche en un point fixe.

Pour les mâles, 15 classes de taille d'intervalle 45.07 µm entre les valeurs minimales de 649 et maximales de 1325 µm.

La distribution générale des classes de taille apparaît plurimodale pour les trois passages (Fig. 3) et homologue au moins en ce qui concerne les classes dominantes: classe 10 (1132-1185 µm) chez les femelles ♀; classe 9 (1009-1054 µm chez les mâles). Elles représentent respectivement 22% des ♀ et 20% des ♂. Ces optimums de taille pourraient caractériser l'ensemble des populations de T. longicornis en période printanière, dans la zone considérée.

Analysée station par station, la distribution des classes de tailles apparaît également plurimodale, indépendamment du temps (Fig. 4).

Pour chacune d'elles, on a recherché la composition précise de la population de T. longicornis. En nous basant sur l'hypothèse d'une analogie entre l'évolution de femelles en élevage et celle d'individus grandissant in situ.

3) Comparaison avec des données biométriques homologues sur des Copépodes en élevage

Des femelles de T. stylifera issues d'oeufs pondus au laboratoire par des ♀ sauvages, ont été élevées dans des conditions stables de température et de nutrition, des stades nauplii au stade adulte. Le développement des oeufs et des stades juvéniles successifs était synchrone (Comm. pers. Nival, en prépar.).

Les valeurs des longueurs, de leur variation dans les élevages synchrones et du facteur d'accroissement (Ac) calculé comme précédemment sont de nature à fournir des informations sur la dispersion "naturelle" des longueurs dans une population contrôlée.

Ces données sont synthétisées sur le tableau II.

Tableau II: *Paramètres de comparaison avec deux lots de Temora stylifera femelles "synchrones", en élevage dans des conditions constantes.*

Lg céphalothorax moy + E. S. (µm)	Cv %	$\frac{\text{Lg min}}{\text{Lg max}}$ (Ac)
1022 + 6 (n=97)	4.09	0.84
986 + 11 (n=34)	4.47	0.85

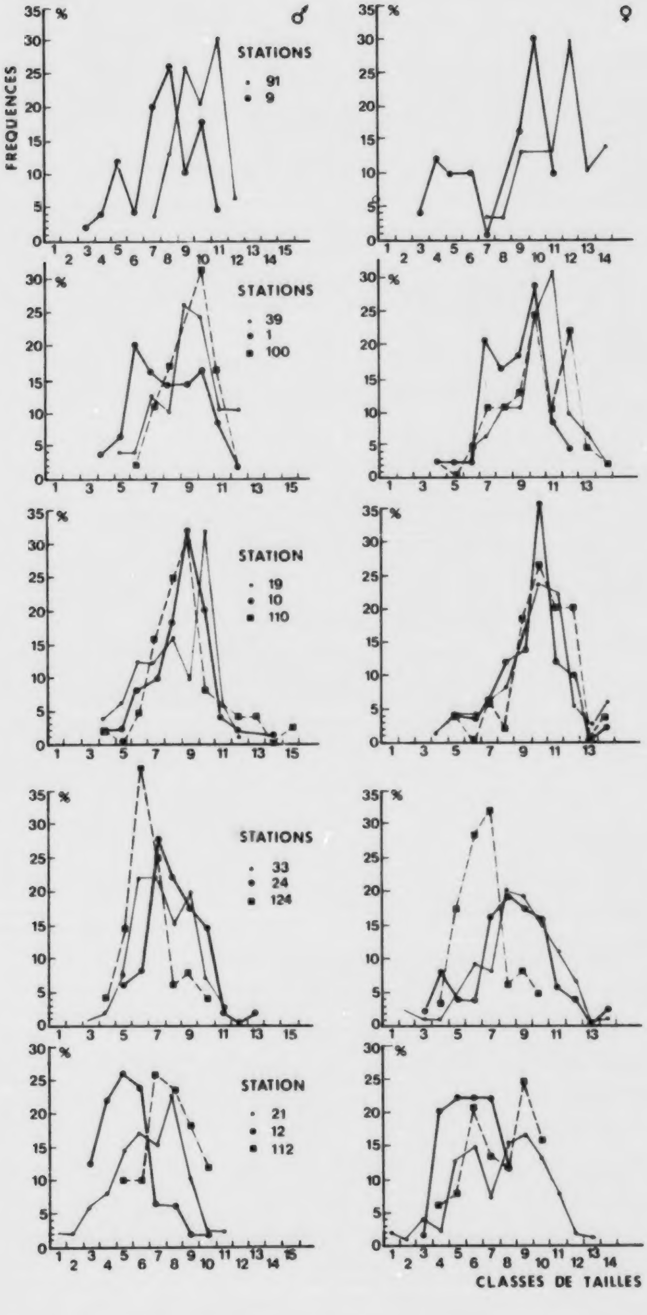

Figure 4. *Fréquence de distribution des classes de taille du céphalothorax, pour chaque station des 3 grilles. (même figuré que fig. 3).*

Les coefficients de variation, de l'ordre de 4%, et les rapports d'accroissement Ac et 0.84 témoignent d'une faible dispersion des longueurs comparables à celle obtenue sur Pseudocalanus en élevage (Lock et McLaren, 1970).

Ces valeurs comparées avec celles obtenues pour T. longicornis "sauvages", ♀ (Ac moyen = 0.65) ou mâles (Ac moyen = 0.71), confirment une hétérogénéité des populations aux différentes stations. Les distances observées entre les pics de fréquences (Fig. 5) dépassant l'intervalle moyen (inférieur à 200 µm), qui correspond à Ac des T. stylifera élevés au laboratoire, suggèrent que ces individus se sont développés dans des conditions extérieures différentes.

Les valeurs des intervalles, observées chez T. stylifera du tableau II (225 µm et 137 µm pour les deux lots) sont comparables à celles des T. longicornis en élevage (Klein-Breteler, com. pers.).

Les histogrammes confirment pour les ♀, aussi bien que pour les ♂ (Fig. 5), un décalage des cohortes dominantes de petites tailles à la côte vers de grandes tailles au large. La disparition de cohortes en fonction du temps (ex. petites tailles entre ECI_1 et ECI_2) étant due vraisemblablement à la mortalité naturelle de populations agées.

DISCUSSION

L'absence de discontinuité importante dans les courbes de taille à chaque station indique qu'il n'y a pas d'apport de populations allochtones et l'homologie relative de la distribution spectrale au cours de trois passages successifs exclut une répartition due au hasard.

De plus, on constate qu'il n'existe pas à cette période de l'année (mai-juin), de mélange important entre les eaux côtières et celles du large, sinon l'ensemble de la zone présenterait une répartition homogène des classes de taille. Toutefois, certaines station de EC_{II} (st. 24, 1 et 9) où les longueurs moyennes des céphalothorax de T. longicornis sont assez similaires pour les classes dominantes des ♀ ou des ♂ pourraient appartenir à la même masse d'eau, de même que les stations du large des grilles EC_I.

D'après ces observations il semble que les variations de longueur du céphalothorax des ♀ et des ♂ de T. longicornis dans un temps réduit, associées à une distribution spatiale côte-large, doivent être attribuées à une évolution locale, à chaque station de la population autochtone de Copépodes.

Les pontes décalées dans le temps, de 24 h à quelques jours ainsi que le montre des élevages (Harris et Paffenhöfer, 1976) conduisent à des cohortes-soeurs qui seront soumises aux variations des températures locales.

Ainsi le long du transect EC_{II} pour une température moyenne de $11^{o}84$ (st. 12) les femelles de T. longicornis sont de petite taille (938 µm), au contraire au large (st. 10), pour une température de $10^{o}70$ la classe dominante atteint 1133 µm (r = -0.76, n = 5) pour l'ensemble des 5 stations EC_{II} une bonne corrélation est obtenue entre la longueur et la température (r = -0.76, n = 5).

De même, l'ensemble des longueurs moyennes des 3 grilles apparaît corrélé à la température moyenne de surface, à la limite de la probabilité 95% (r = -0.51, n = 14), les températures intégrées pour la colonne d'eau aux différents points, se situent entre 10^{o} et $10^{o}5$ pour le premier passage, 10^{o} et $11^{o}2$ pour le second et $10^{o}70$ à $11^{o}84$ pour le troisième.

Par contre, pour les transects du mois de mai où les températures moyennes aux stations sont plus stables, les relations longueurs - t^{o} n'apparaissent pas, sauf entre les stations homologues 33 et 124 (les longueurs moyennes sont significativement différentes pour une différence de température de 1^{o}).

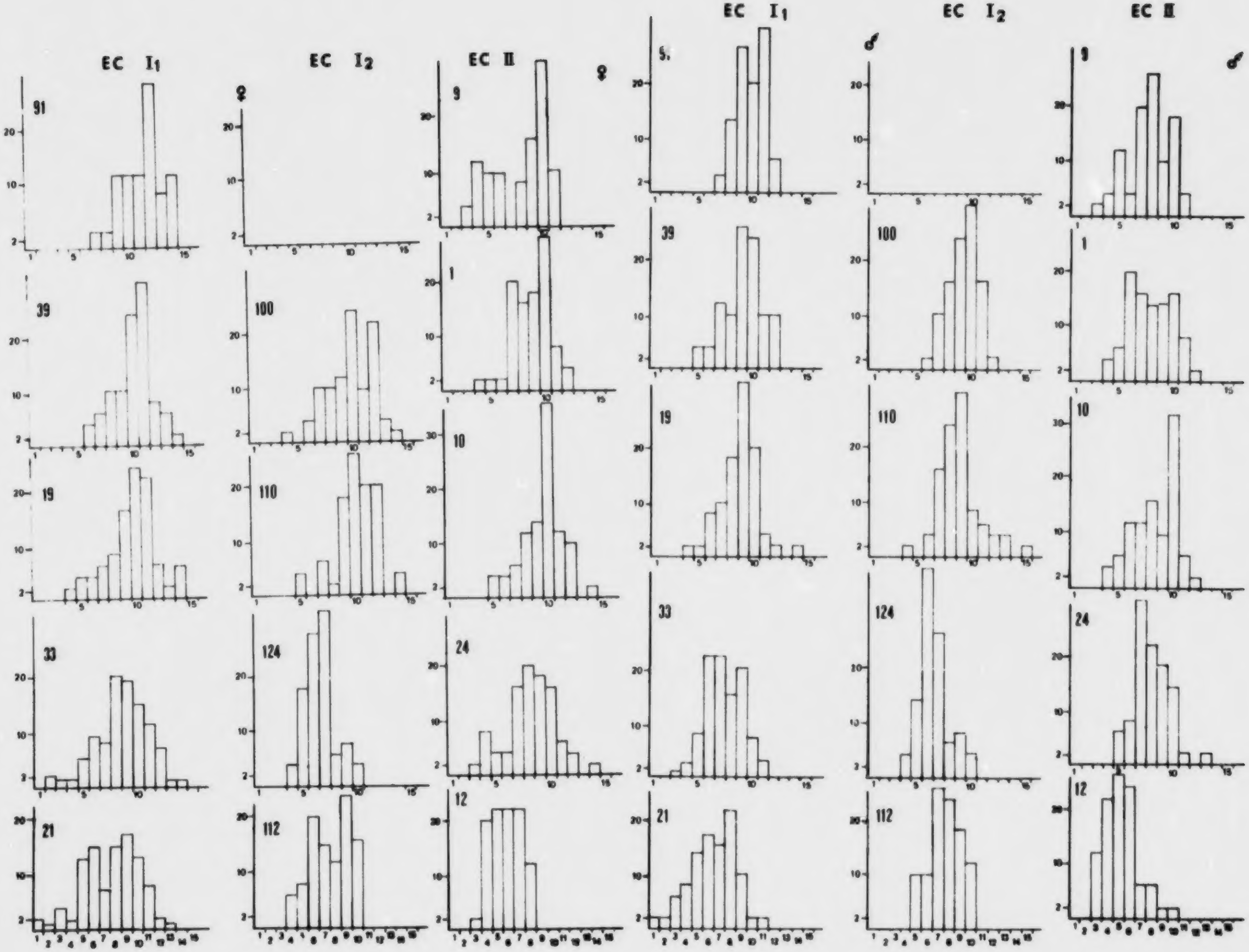

Figure 5. *Distribution des classes de tailles des femelles et des mâles de T. longicornis à chaque station, pour les 3 passages (fréquences en ordonnée; classes de taille en abscisse).*

En Mer du Nord, Evans (1981) attribue aux variations d'abondance d'une espèce dominante de diatomées les variations de taille des T. longicornis: cette espèce ne serait pas exclusivement température - dépendante pendant sa croissance.

En élevage, Klein-Breteler et al. (1982) observent un accroissement de la longueur en fonction de la concentration alimentaire moindre chez T. longicornis (11%) que chez Centropages hamatus (accroissement de 33%).

La distribution des classes de taille le long du transect étudié peut être considérée comme représentative de la partie orientale de la Manche aux variations locales près, résultant de l'évolution de facteurs hydrobiologiques à petite échelle. Mais la température ne serait qu'un des facteurs déterminants (Lock et McLaren, 1970), chaque cohorte exprimant sa taille optimale, traduite par la fréquence maximale de la classe de taille, en fonction des conditions globales du milieu.

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A RE-EVALUATION OF THE FAMILY CLETODIDAE SARS, LANG (COPEPODA, HARPACTICOIDA)

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Abstract: A proposal is being made to dismantle the artificial harpacticoid family Cletodidae Sars, Lang and to redistribute its over 40 genera into new family units. These are: Paranannopidae fam. nov., Huntemanniidae fam. nov., Rhizothricidae fam. nov., Argestidae fam. nov., and Cletodidae s. str.. For several genera the inclusion in the family Canthocamptidae is proposed, either as a new subfamily Hemimesochrinae or in other cases **incertae sedis**. A revision of the superfamilies is needed as well as a general rediscussion of the Langian system of the Harpacticoida.

INTRODUCTION

With more than 40 genera, Cletodidae Sars, Lang is probably the most heterogenous family of the Harpacticoida. Because of its importance on the muddy bottoms, new genera are being described almost yearly, since the study of deep-sea collections started.

Lang (1936) recognized several "Entwicklungslinien" within the family however he did not develop this idea further. In 1948 he considered the Cletodidae to be a family "in statu nascendi". Taking a different view, Becker (1972) considered the Cletodidae to be an artificial, paraphyletic assemblage of very old genera.

Taking up an idea mentioned previously (Por, 1984) and based on new material (Por, in press), I tried to develop some of the ideas of Lang and of Becker and to reallocate 39 genera of "cletodid" harpacticoids to new family units. Of these genera, Beckeria Por, Scintis Por and Megistocletodes Por are new genera (Por, in press).

Dahlakia (Por) stands for Cletocamptus xenuus Por, 1968. Nannopodella Monard is insufficiently described. Pyrocletodes Coull is a tetragonicipitid (Dinet, 1976), Taurocletodes Kunz, a junior synonym of Parepactophanes Kunz (Wells, 1979) and Monocletodes Klie a synonym of Metahuntemannia Smirnov (1946). Austrocletodes Pallares, Pontocletodes Apostolov and Miroslavia Apostolov have been unknown to me at the time of this analysis.

Rather then designating the most typical genus as the type genus of the new families, I preferred to use the name of the genus which seems to be the most primitive of the "Entwicklungslinie". In the fluid stage of the cletodid taxonomy, this is perhaps preferable.

REDISTRIBUTION INTO FAMILIES

1. Paranannopidae new family. This family, first sketched out by Becker (1972) contains the genera Paranannopus Lang and Cylindronannopus Coull.

Diagnosis. Females. Body shortened and robust, segments bare. Furca short. Rostrum rounded-quadratic with sensory setae. Antennula stout of 4 to 6 segments, setae strongly pennated. Antenna two-segmented, exopodite big, of three segments or gradually fused, with 5 to 7 strong setae. Mandibular palpus with broad basis, bearing exo- and endopodite. Maxillula with exo- and endopodite. Maxilla with 4 endites. Maxillipede weak with two robust setae on basis. P I exopodite three-segmented, endopodite two-segmented, non-prehensile. P II - P IV with three-segmented exopodites; endopodites reduced from three-segmented to total absence. P V an unique, more or less quadratic plate. Genital field of complicated structure, with a pair of relatively large receptacula seminis.

Males have been described without knowing the respective females. Shape of body is much more elongated than in the females. Endopodites of P II and P III, tri-articulated, with spiniform process on median segment.

Parananopidae are typical inhabitants of bathyal and abyssal muds morphologically adapted to fossorial life. Sexual dimorphism of body shape, if proven in more species may be very characteristic.

2. Huntemanniidae new family. This family is being established to contain the species-rich genus Metahuntemannia Smirnov as well as Huntemannia Poppe, Beckeria Por (in press), Nannopus Brady, Pontopolites T. Scott and probably Pseudocletodes T. and A. Scott.

Diagnosis. Females. Body relatively small, stout or elongate without important spinulation. Furca short and sometimes strongly modified. Rostrum prominent and showel-shaped. Antennulae, short and strong, 5- or 6-segmented with pennate setae. Antenna two-segmented. Exopodite one-segmented or absent. Mandibular palp broad, without exopodite and endopodite small or missing. Maxillula without exo- and endopodite. Maxilla with 3 endites. Maxillipede normal or reduced. P I with strong fossorial exopodite with tendency to fuse into one segment; endopodite reduced or absent. P II - P IV exopodites unmodified but endopodites (apart from Metahuntemannia peruana) reduced or lacking altogether. P-V with plate-like basi-endopodite and small or fused exopodite.

Males. The males of Metahuntemannia may present a more elongate body shape, however the respective females are often unknown. Also they have reduced mouthparts and less modified P I. Common to all the family is the dimorphic three-segmented P III endopodite, with dimorphic features on the median segment.

Pseudocletodes has a differently built P V, a fact that makes its position somewhat uncertain. Eventually the Paranannopidae and Huntemanniidae may be very closely related. The Huntemanniidae are endopelic animals of cold or deep environments. The primitive Nannopus is a cosmopolitan brackish water genus.

3. Rhizothricidae new family. This is a third family containing Rhizothrix Brady and Robertson and Tryphoema Monard.

Diagnosis. Females. Cylindircal body, covered by a dense pubescence. Furca rounded or produced into a spiniform process. Rostrum in general not prominent. Antennula with 4 to 6 segments and pennate setae; last segment with strong apical spine. Antenna two-segmented with uni-articulated exopodite. Mandibula only with endopodite. Maxillula variable, with or without exo- and endopodite. Maxilla with 3 endites. Last exopodite and endopodite segments of P I bear two long apical setae each, with big apical brush. P II - P IV with 2- to 3-segmented exopodites; endopodites 2- or 1-segmented. P V of both sides fused, broad basi-endopodite and small exopodite; both branches bear strong and richly pennated setae.

Males with chirocerous antennula. No known dimorphism of swimming legs. PV strongly reduced.

The Rhizothricidae inhabit shallow bottoms of mixed sediments. The peculiar brushes of the P I must have a specific role (in feeding?).

4. Argestidae new family. This family comprises the following genera: *Argestes* Sars, *Argestigens* Willey, *Fultonia* T. Scott, *Parargestes* Lang, *Neoargestes* Drzycimski, *Mesocletodes* Sars, *Leptocletodes* Sars, *Eurycletodes* Sars, *Hemicletodes* Lang, *Corallicletodes* Soyer, *Hypalocletodes* Por, *Odiliacletodes* Soyer, *Dizahavia* Por and *Megistocletodes* Por (in press). In this large family there is much evolutionary distance between the primitive and the advanced genera; this fact is reflected in the family diagnosis.

Diagnosis. Females. Relatively big forms with dorso-ventrally slightly flattened non-tapering body. Integument is poorly chitinized and intestine usually shows through. Segment edges often denticulated and always strongly spinulated. Last abdominal segment squarish, length/width ratio about 2/3. Operculum relatively proximal, situated slightly below the middle of the segment. Furcal branches set wide apart at the corners of last abdominal segment, of variable length. Rostrum triangular, as a rule not articulated. Antennula 8- to 6-segmented without pennate setae. Antenna two- or three-segmented, exopodite uni-articulated small or missing. Manidbula initially with exo- and endopodite, but as a rule only with the latter. Maxillula without exo- and endopodite. Maxilla with 4 and mostly with 3 endites. Maxillipede normal or reduced in *Mesocletodes*. Legs situated wide apart, elongated; P I exopodite three-segmented; endopodite initially three-segmented, as a rule two-segmented or even reduced to one segment.

Three-segmented exopodites of P II, P III and P IV with a tendency to be considerably elongated; number of endopodite segments is gradually reduced, as a rule correlatively with the elongation of the exopodites. When endopodites are reduced, first segment is very small. P V as a rule with narrow elongated exopodite and a non-prominent basi-endopodite. The basi-endopodite is broad and prominent in *Odiliacletodes* and *Hypalocletodes*.

Males are unknown in the majority of the species. They are known only in four species of *Eurycletodes*, in *Argestes* and *Hypalocletodes*. In the first genera only P V is slightly modified and smaller than in the female; in *Hypalocletodes* the males have subchirocerous antennula and strongly modified P V. Parthenogenetic species or extremely poecilandric populations are the rule in the family.

The Argestidae are epi-pelic dwellers of cold water; soft and flat body but especially "spider-like" elongation of legs and furca are characteristic.

5. Cletodidae sensu strictu. This family contains the following genera: *Enhydrosoma* Boeck, *Cletodes* Brady, *Enhydrosomella* Monard, *Acrenhydrosoma* Lang, *Stylicletodes* Lang, *Australonannopus* Hammond, *Barbaracletodes* Becker, *Scintis* Por (in press) and *Limnocletodes* Borutzky.

Diagnosis. Females. Body small as a rule, cylindrical and well chitinized, segments well defined and edges spinulated. When preserved, body has a typically arched shape. Furcal branches elongated, basically pyriform, with considerable intraspecific polymorphism in size and shape. Rostrum as a rule articulated, triangular and often bifid. Antennula 7- to 4-segmented, last segment considerably elongated; pennate setae may be found. Antenna two-segmented, exopodite uni-articulated or absent. Mandibula and Maxillula with no exo- and endopodite (exception in some *Cletodes*). Maxilla with 3 endites. Bases of legs are transversally trapezoidal and the two branches are articulated at a distance from each other. P I with 3-segmented exopodite and 2-segmented endopodite (in *Scintis* endopodite reduced). PII-PIV with 3-segmented exopodites (one segment lacking in *Enhydrosomella*) and 2-segmented endopodites (one endopodite segment in some *Enhydrosoma* and endopodite IV absent in *Australonannopus*). Endopodites characterized by short first segment and elongated, rod-shaped second segment. Second segment with two or three long apical setae only. P V well developed and chitinized, with a complicated tri-dimensional structure. Shape and size of P V polymorphic within the same population.

Males have a considerable dimorphism of operculum and furca. Antennual subchirocerous. Endopodite P III three-segmented with median segment protruding in a spine. In some cases there is no leg dimorphism. P V very different from female.

The Cletodidae sensu strictu are active mud-burrowers known mainly from shallow and sublittoral, often mixed bottoms. They move through energetic body movements. The widespread, brackish Limnocletodes as well as Scintis and Australonannopus have a somewhat peripheric position in the family.

6. Hemimesochrinae new subfamily of Canthocamptidae Sars, Monard, Lang. Lang (1948) put much weight on the non-prehensile P I endopodite in order to separate from the Canthocamptidae several genera which he preferred to locate with the Cletodidae. However Nannomesochra Gurney has been left with the Canthocamptidae, despite not having an elongated P I endopodite.

I propose to collocate the following genera in a subfamily of the Canthocamptidae: Nannomesochra Gurney, Hemimesochra Sars, Heteropsyllus T.Scott, Mesopsyllus Por, Poria Lang and Dahlakia Por (nom. nov. for Cletocamptus xenuus Por, 1968). Pending a more general discussion on the subdivisions of the Canthocamptidae, only the characteristic features of the proposed subfamily are presented.

Diagnosis. Females. Small animals of slightly pyriform habitus. Furca only slightly elongated. Antennula 7- to 5-segmented with swollen first or first and second segments. P I endopodite non-prehensile; in many species the inner seta of the first endopodite segment is turned upward and penicillated. Endopodites of swimming legs with first segment equal or subequal with the following one. P V of the canthocamptid type but with a tendency of fusion of the branches; in some species one of the basi-endopodite setae is especially long and forms a sling with its symmetrical seta of the other side. Basi-endopodite frequently with a hyaline field. Receptaculum seminis of the canthocamptid type but more compact and rounded.

Males, as far as known have haplocerous antennula. P II is not modified, P III is modified and three-segmented or two-segmented (in Nannomesochra). P V with fused branches.

The subfamily is formed of marine soft-bottom genera. Another big marine canthocamptid genus, Mesochra Boeck is characterized by elongated P I endopodite, like the bulk of the family. One may speculate that this feature became important only with the transition of the Canthocamptidae to life on phytal substrate. Incidentally, the genus Moraria, a subterranean freshwater genus does not have a "prehensile" P I.

Earlier authors, especially Borutzky (1952) considered the need of dividing the Canthocamptidae into subfamilies.

7. Canthocamptidae incertae sedis. Pending a revision of the Canthocamptidae, several other "cletodids" should be placed into this family. These are Cletocamptus Schmankewitsch, Parepactophanes Kunz, Leimia Willey, Hemimesochra rapiens Becker and Heteropsyllus serratus Schriever. These taxa will be in good company with several marine canthocamptids which also await a revision (e.g. Orthopsyllus Boeck, Itunella Gagern, Ophirion Por, Psammocamptus Mielke, etc.).

GENERAL CONSIDERATIONS

Lang (1948) placed much weight on features like numbers of appendage segments and leg-setation. Soyer (1964) stressed the importance of other "non classical features" like general body shape. Becker (1972) used much, but warned also from the excessive use of morphological adaptations representing ecological convergence.

It is now well known that segment and setation reduction is a general evolutionary trend in all the copepod lineages. Therefore in a large complex of genera also other features have to be considered. First of all the cletodids are almost without exception mud-dwellers: as exposed above, the different families represent different "approaches" to benthic life on soft bottoms: Paranannopidae and Huntemanniidae are rowing-fossorial animals; Argestidae have "epi-pelic" "spider-like" adaptations; Cletodidae s. str. are animals moving with "nematode-like" bends of the body. All these ecological adaptations have deep consequences on the different morphological features.

The new families have also different "sex linked" characters: Paranannopidae and Huntemanniidae have (probably?) a very dimorphic body shape; Argestidae are parthenogenetic and the few known males are barely dimorphic; Cletodidae s. str. have extremely polymorphic furca and P V.

Taking into account that the only positive character used by Lang (1948) to define his Cletodidae is the lack of elongation of the first endopodite segment of P I - also an ecologically adaptative feature - the proposed new families have much more consistency than the old complex.

Such a revision of the Cletodidae has its repercussion also on the supra-familiar taxonomy of the Harpacticoida. For instance suprafamily Cletodoidea Bowman and Abele, 1982 has no reason of existence. Its other component, the Laophontidae and Ancorabolidae, should form a suprafamily Laophontoidea. The families of the old cletodid complex could be redistributed in the following way: Paranannopidae, Huntemanniidae and Rhizothricidae probably belong to the Tachidoidea; the Argestidae and the Hemimesochrinae to the Ameiroidea. The Cletodidae s. str. should eventually be placed in a new suprafamily Cletodoidea s. str.!

All this can mark the opening accords for a general revision of the Langian system of the Harpacticoida. A new key to the families should probably wait for this revision.

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CHEMORECEPTION, NUTRITION AND FOOD REQUIREMENTS AMONG COPEPODS

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Abstract: Analysis of theoretical concepts and of recent experimental findings related to the diffusion, chemoreception, ingestion and assimilation processes are provided with references to the food requirements of copepods and Artemia. The relationships existing between these different phases of the feeding process are discussed.

It is hypothesised that the influence of the chemosensory and ingestion processes on growth depends on the ability of the food to satisfy the various requirements of the organisms.

INTRODUCTION

Food requirements, feeding behavior, ingestion and assimilation of filter-feeding copepods are known as paramount process involved in the transformation of organic matter between the primary and secondary marine trophic levels. In order to understand and thus, to measure the various steps leading from primary producers to the growth of the consumers, we must define conceptual models based on actual observations and few biological and structural properties to which the copepod's life is strictly linked. Among these properties, the following ones appeared to be extremely relevant:

- 1 - Copepods live in a nutritionally dilute environment (Conover, 1968);

- 2 - Swimming and feeding in copepods are interdependent (Cannon, 1928; Gauld, 1966; Kerfoot, 1978; Strickler, 1982; Yule and Crisp, 1983;)

- 3 - The expenditure of energy on swimming and food gathering is expected to be geared to the concentration of food stock available (Lam and Frost, 1976);

- 4 - Energy needed to cover metabolic requirements, growth and reproduction is exclusively dependent on the acquisition of organic matter present as food in the water (i.e. reviews by Marshall, 1973 and Conover, 1978).

Copepods are exposed to variable food concentrations due to variable algal production, patchiness and vertical migration. The functional response of filter-feeding copepods to food concentration has been studied extensively. Mullin et al. (1975) found that a Michaelis-Menten function of the feeding rate versus increasing food concentration yielded one of the best models.This model has become popular in the literature, even though the adequacy of other models such as Holling's functional curves has also been discussed (Conover and Huntley, 1980). Actual models describing the feeding process in grazing copepods are mechanistic (i.e. Lam and Frost, 1976; Frost, 1977) and have tended to consider filter-feeders as passive leaky sieves, with prediction of feeding rates exclusively based on the size and concentration of particulate food.Now that we know the complex behavior used by copepods (Rubenstein and Koehl, 1977; Poulet and Marsot, 1978, 1980; Alcaraz et al, 1980; Strickler, 1982) new feeding models should emerge based on more realistic assumptions.

If we assume that uptake and transformation of organic matter in the marine food web lead to the optimization of secondary production, we ought to know the mechanisms allowing copepods to cope with the 4 properties listed above such that production can be achieved. Our understanding of the food-gathering process and food transformation into secondary production is not simply a matter of energy gain, or optimal foraging, expressed in term of calories per unit of time (Schoener, 1971; Lehman, 1976; Taghon, 1981). It also relies on groups of mechanisms based on biochemical and physiological processes, as outlined in the diagrams in Figs. 1A and B. Our first conceptual model (Fig. 1A) is based on chemoreception considered as a functionnal link between phytoplankton and zooplankton. It relies on specific chemicals released by the food source, acting as chemical signals when diffusing in the surrounding water and which promotes a behavioral reaction of the copepods when reaching the chemoreceptors. It is also assumed that these organisms possess specific chemoreceptors permitting the perception of the chemical information. The mechanism leading a chemical information to a behavioral response is known as transduction and it can be recorded by electrophysiological technics (Mackie and Grant, 1974; Galifret, 1978). From a serie of morphological studies of receptors (Ong, 1969, Friedman and Strickler, 1975; Friedman, 1980; Gill, 1983), behavioral feeding experiments (Poulet and Marsot, 1978, 1980; Donaghay and Small, 1979; Cowles and Strickler, 1983) and cinematographic observations (Alcaraz et al, 1980; Koehl and Strickler, 1981) it becomes clear that this model is a realistic framework.

The second conceptual model (Fig. 1B) based on the assimilation of food is an attempt to relate food standing stock and metabolism of the consumers. The assumption is that the level of the metabolism is also food dependent. For example, copepods facing a low food level condition (i.e. - the limiting factor) will have to reach low metabolism (i.e. diapause) and consequently will stop production (i.e. - growth, egg production), or should move to locations where food is more abundant. On the other hand, it is assumed that growth reaches maximum rates at food concentration increasing and reaching saturation, parallel to metabolism increase. The continuum between diapause and growth is a matter of temporal succession (i.e. - diurnal; seasonal variations). Depending on the digestive enzyme activity which is presumably in phase with food stocks encountered in the environment (Boucher and Samain, 1974; Mayzaud and Poulet, 1978; Cox, 1981) the amount of food channelled into growth should vary. Recent studies on the digestive enzyme activity (Cox, 1981; Head and Conover, 1983; Mayzaud et al, 1984; Baars and Oosterhuis, 1984) related to the concentration, availability and temporal variation of food, support the contention that food standing stock and metabolism of copepods, and so indirectly growth, are related through digestive enzymes.

The structural position of the two block diagrams (Fig. 1A, B) with reference to copepods are different. Copepods are considered as intermediate operators between the external environment, where chemoreception serves as a tool for food searching and selection, and the internal milieu, where assimilation contributes to the transformation of the ingested food (Fig. 2). Chemoreception and assimilation being interfaced by ingestion. Due to its intermediate functional position, ingestion (I) (Fig. 2) may be the central step between the chemoreception and assimilation activities of copepods. This diagram presumes that chemoreception, ingestion and assimilation work in a continuum allowing the transformation of organic matter originating from the primary producers.

Some properties and mechanisms involved in these two conceptual models form the subject of this paper.

FIG.1_A

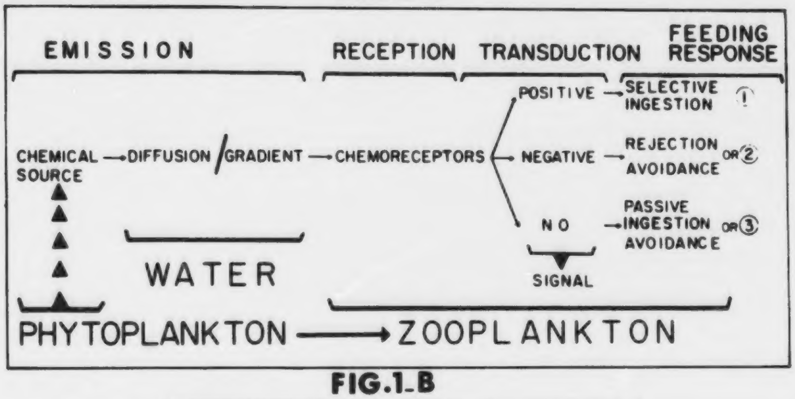

EMISSION
RECEPTION
TRANSDUCTION
FEEDING RESPONSE
POSITIVE
SELECTIVE INGESTION
①
CHEMICAL SOURCE
DIFFUSION
GRADIENT
CHEMORECEPTORS
NEGATIVE
REJECTION OR AVOIDANCE
②
PASSIVE INGESTION OR AVOIDANCE
③
NO SIGNAL
WATER
PHYTOPLANKTON
ZOOPLANKTON

FIG.1_B

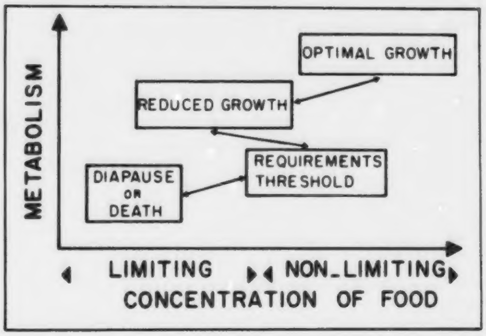

METABOLISM
OPTIMAL GROWTH
REDUCED GROWTH
REQUIREMENTS THRESHOLD
DIAPAUSE OR DEATH
LIMITING
NON_LIMITING
CONCENTRATION OF FOOD

FIG.2

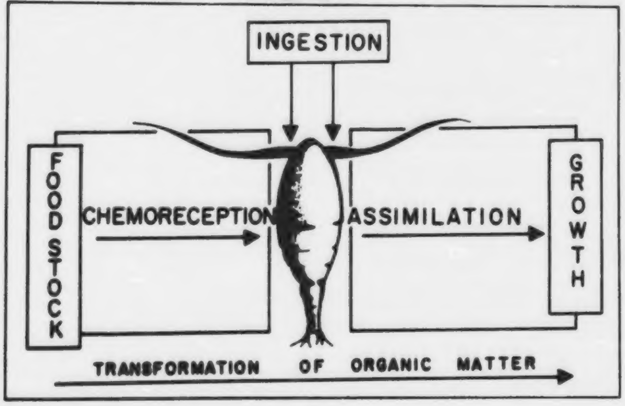

INGESTION
FOOD STOCK
CHEMORECEPTION
ASSIMILATION
GROWTH
TRANSFORMATION OF ORGANIC MATTER

Figure 1 A. *Flow diagram of a chemosensory model relating phytoplankton and zooplankton through chemically mediating feeding relationships and resulting types of feeding responses. Some examples of the behavioral feeding responses of copepods have been given by: 1 - Poulet and Marsot (1978); Donaghay and Small (1979); 2 - Fiedler (1982); Huntley (1982); 3 - (ingestion of oil droplets) Conover (1971); Berman and Heinle (1980).*

B. *Diagram of the food-metabolism model. It is assumed that metabolism is food dependent.*

Figure 2. *Conceptual framework of the transformation of organic matter between phytoplankton and copepods representing the central position of ingestion between the chemoreception and assimilation processes leading to growth.*

I. THE CHEMOSENSORY MODEL

The definition of chemoreception and description of the chemosensory behavior of a number of marine organisms ranging from algae to fish have been documented in the past (Mackie and Grant, 1974; Laverack, 1974; Levandowsky and Hauser, 1978; Gauthier and Aubert, 1981; Mackie, 1982). In comparison, the study of the chemosensory mediated feeding relationships between phytoplankton and zooplankton is still at its early stage of investigation. However, initial results for both marine and freshwater zooplankton have outlined some of the physical, chemical and behavioral factors involved in this process (i.e. Kittredge et al., 1974; Poulet and Marsot, 1980; Porter and Orcutt, 1980; Koehl and Strickler, 1981; Poulet and Ouellet, 1982; Andrews, 1983). In the field of plankton the advancement of chemoreception has encountered several technical difficulties related to the measurement of dissolved molecules at the very low level (10^{-9} M); the concentration threshold at which copepods respond and the proper way to describe copepod behavior. The usage of a series of new tools, such as high performance liquid chromatography (i.e. Poulet and Martin-Jezequel, 1983), photographic or cinematographic observations (i.e. Alcaraz et al., 1981; Poulet and Ouellet, 1982; Price et al., 1983; Gill, 1983) and pneumograph records (Yule and Crisp, 1983; Gill, 1983) now allows us to evaluate more accurately each step involved in this mechanism. Still, the finding of molecules having a stimulatory effect on copepods remain to be achieved on a broader scale.

Hellebust (1974) has reviewed the types of extracellular chemicals metabolized by phytoplankton. Among these compounds, amino acids are released in the water at rates changing with the growth phase of the cells (Hammer et al., 1981; Poulet and Martin-Jezequel, 1983). These compounds have been assayed in feeding and locomotion experiments and they were classified as attractant and stimulant pheromones for zooplankton (Fuzessery and Childress, 1975; Hamner and Hamner, 1977; Poulet and Marsot, 1980; Poulet and Ouellet, 1982). However, the direct link between the sensory response of copepods and these molecules including their phytoplankton origin and their concentration in nature has not yet been established. We postulate that these compounds in nature may also trigger behaviors similar to those observed in the laboratory (Hamner and Hamner, 1977; Poulet and Marsot, 1980; Poulet and Ouellet, 1982) without excluding the potential activity of other types of molecules such as peptides, carbohydrates, fatty acids, vitamins. Because of our background in the study of the role of amino acids in the chemoreception of zooplankton, we used this category of compounds to test the chemosensory model.

Looking at the left side of the diagram in Figure 1 A, we question how amino acids from the phytoplankton source are creating a chemical gradient, reach copepod's chemoreceptors and finally promote behavioral responses. In order to answer these questions a series of models were developed in the past for a variety of organisms of both terrestrial and marine origin (see review by Okubo, 1980). Originally described by Bossert and Wilson (1963) for atmospheric problems of communication among ants, the models used to determine the range of these parameters can be utilized for copepods as well. Recently, Andrews (1983) has applied such models to investigate the effect of advection in copepod feeding currents. He showed that the warning received by a copepod of an approaching algae is a function of the radius of the active space, the detection threshold, the position of the algae in the stream field and the molecular diffusivity of the exudate. All these parameters are paramount to the analysis of olfactory communication among organisms. However, depending on the nature of the fluid and on the velocity fields created in the water by the feeding appendages of copepods, these models must be slightly modified as Bossert and Wilson (1963) and Andrews (1983) pointed out. The difference between chemoreception in air and water relies on the fact that in the water, the molecules are moved in the direction of the flow which is considered as laminar in the model (Reynolds number $R \leq 1$; Purcell, 1977; Koehl and Strickler, 1981). That is, the movement is resisted by viscosity, not by inertia. Under such conditions, the transfer of molecules from their source to the chemoreceptors is related to diffusion rather than to flow alone (Berg and Purcell, 1977). The flow field created in the surrounding while copepods are swimming and feeding (Strickler, 1982) is formed of layers of liquid which carry particles and molecules practically stationary with reference to the fluid itself. Molecules must cross the boundary layer by diffusion before reaching the surface of the chemoreceptor in order to trigger the copepod's response. In other words, molecules are carried close to the vicinity of the copepods by advection of the fluid and they reach the chemoreceptors by diffusion.

It is assumed that phytoplankton cells release amino acids instantaneously in the stream of water, which is still water relative to the molecules. The equations used in the model will be then, similar to those given by Bossert and Wilson (1963, p. 445-446). Following these author's definitions, the expanding sphere of diffusing molecules will remain centered on the phytoplankton cells in our case; or else be carried along with moving fluid creating a non-spherical volume, like in the case discussed by Andrews (1983). Suppose Q molecules are released at the origin of a cartesian coordinate system, center of the cell, at time $t = 0$. The concentration U, in space through time is given by:

(1)

$$U_{(x,y,z,t)} = \frac{Q}{(4\pi Dt)^{3/2}} e^{-r^2/4Dt}$$

where $r^2 = x^2+y^2+z^2$ is the position of the cell in a tridimentional space, D is the diffusion coefficient and Q is the number of molecules released by the phytoplankton. Equation (1) assumes that molecules are free to diffuse in all directions. Let K be the threshold concentration of molecules at which copepods, receiving the pheromone, respond to the chemical signal. According to Bossert and Wilson (1963) the surface of concentration K, in space at time t, is a sphere with center at the origin and radius

(2)

$$R_{(t)} = 4\ Dt.\ \log \left(\frac{Q}{K\ (4\pi Dt)^{3/2}} \right)$$

This sphere is the active space, defined as the volume where the concentration (U) of the stimulatory molecules is equal or higher than the sensory threshold (K) triggering the copepod's behavior. This space is also defined as the warning space of copepods (Andrews, 1983). The radius of the expanding sphere through time increases to a maximum given by the equation:

(3)

$$R_{\max} = \sqrt{\frac{Q}{K} \quad \frac{3}{2\pi e}}$$

The values for D, Q and K were tentatively assumed by Andrews (1983) who did not define the nature of the chemical operating in his model. For amino acids, we are able to test real values in the model. The diffusion coefficient, at 25°C, is: $D = 1 \times 10^{-5}\ cm^2.s^{-1}$. The values for K are borrowed from Fuzessery and Childress (1975), Poulet and Ouellet (1982) who experimentally found that the range for zooplankton is 10^{-8} M to 10^{-2} M. More difficult is to evaluate Q. We have recently measured Q for natural phytoplankton assemblages, during shipboard incubations achieved offshore Brittany (France), with reference to the amino acids (Poulet, Videau, Martin-Jezequel, unpublished). It was found that in the vicinity of the cells, Q ranged from 0.3×10^{-6} to 5×10^{-6} mole.cm^{-3}. Putting all these data in equation (3) we obtain the values for R_{max}. The results (Table 1) show that for amino acids, the radius of the active space varies from 0.005 to 2.7 cm, depending on both the level of sensibility of copepods and the amount of molecules released by phytoplankton. This active space is roughly 27 times broader than the length of an "average" copepod 1 mm in size. Therefore, the chemical concentration (U) originating from surrounding phytoplankton could be theoretically perceived by copepods for $U \geqslant K$ in any direction of space given by x, y or $z \leqslant R_{max}$.

It is interesting to compare these values found for the chemical active space of a copepod to similar boundaries related to a physical stimulus, such as a weak water jet (1.5 $cm.s^{-1}$), which has been experimentally measured by Gill (1983) (Fig. 3 A,B). She found that the response (escape reaction) of copepods to the jet was related to the speed of the water jet, the position of the jet relative to the copepod, and mechano-receptors located on the first antenna. The percentage of copepods responding to jets with antero-posterior flow varied from 0 to 100 % depending on the immediate area around the copepods. The area obtaining more than 50 % responses is an arc of a circle with $\theta = 180^{o}$, with a radius $R < 0.45$ cm, corresponding to the anterior-lateral region (Fig. 3 A). Similar evaluations of avoidance reaction have been experimentaly obtained with other species of copepods (Haury et al., 1980).

In figure 3 B, circles corresponding to the chemical active space having a R_{max} radius computed from equation (3) (Table 1) are plotted. Within the ranges of Q and K values used, we found that to a first approximation, the dimension of the chemical active space is much broader than the area where a physical stimulus (i.e. water jet) is perceived. However, within the average range of concentrations measured in nature for dissolved free amino acids (10^{-7} M $< U <$ 10^{-5} M; i.e. Dawson and Liebezeit, 1981) and taking $K \mp U > 10^{-7}$ M, it is clear that both physical and chemical active spaces are of the same order of magnitude (Table 1, Fig. 3 A, B). The assumption that mechanoreception and chemoreception in copepods might have similar sensory ranges with space remains to be tested.

The probablility for a particle entering the active space of a copepod to be successively captured and ingested is obviously higher than outside the immediate area defined in Figure 3. It will depend on the encounter rate. Let Zp be the encounter rate, as given by Gerritsen (1980) through the equation

$$Zp = \frac{\pi R^2 N}{3} \cdot \left(\frac{U^2 + V^2}{V}\right) \tag{4}$$

where N is the number of particles per unit volume ($p.ml^{-1}$), U and V are the velocities ($cm.s^{-1}$) of the particles and of the copepods, respectively; and R is the radius (cm) of the active space. Assume $U = 0$ and $V = 0.5$ $cm.s^{-1}$ which is roughly an average cruising speed for feeding copepods (see review by Gill, 1983); and, let N range from 1 to 100 $particles.ml^{-1}$ (corresponding to oligotrophic and pre-bloom conditions), we get values for Zp falling between 2.5×10^{-4} and 1152. The encounter rate changes with the density of particles (Figure 4). Within the range of the active space (R max) comprised between 0.05 cm and 0.7 cm, we found that $Zp > 50$ %, whatever the number of particles. These results mean that under changing conditions of food density, copepods must adjust the radius of the active space, thus, their sensory threshold accordingly to the density of particles so that the encounter rate remains high. This strategy, if it occurs, presumes that chemoreception must be gradually tuned to the variable concentration of the chemical signals, rather than being an on-off process adjusted to a fixed value of K. The results in Figure 4 also suggest that chemoreception when operating at low sensory levels ($K < 10^{-7}$ M, Table 1) might be an advantage for copepods feeding on algae under low density of food, simply because Zp is a function of R^2 max. It is worth remembering that water currents observed around swimming copepods are vorticies 0.9-1 mm in diameter (Gauld, 1966; Strickler, 1982; Yule and

FIG. 3

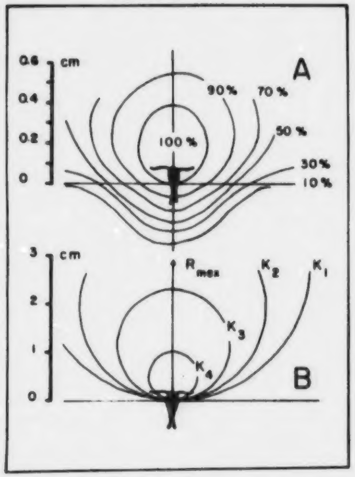


FIG. 4

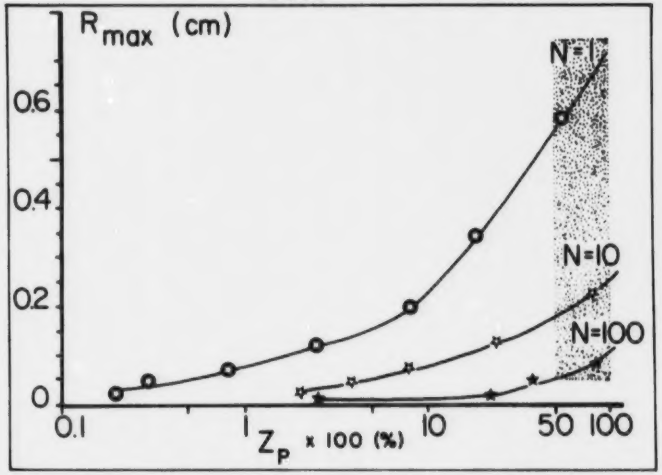


FIG. 5

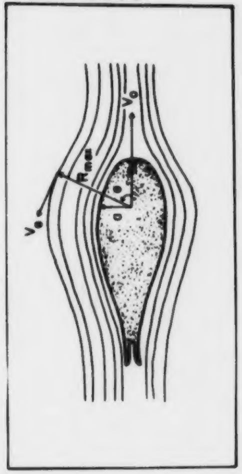


Figure 3. *Ranges of the active space of copepods.* ***A:*** *Physical stimulus. Contour lines of the percentages of copepods responding to weak water jets (1.5 cm.s^{-1}) with escape reaction (After Gill, 1983).* ***B:*** *Chemical stimulus. Contour lines and radius (Rmax) of the concentration thresholds of amino acids to which zooplankton and copepods are responding (i.e. Fuzessery and Childress, 1975; Poulet and Ouellet, 1982). $K_1 = 10^{-8}$ M; $K_2 = 10^{-8}$ M; $K_3 = 10^{-7}$ M; $K_4 = 10^{-6}$ M.*

Figure 4. *Relationships between the radius (R_{max}) of the active space and the encounter rate (Zp) of copepods exposed to variable concentrations of food (N = number of particles.ml^{-1}).*

Figure 5. *Flow lines and fluid velocity (V_θ) in the immediate area around a copepod swimming through the water at low Reynolds' number (R < 1) and at a constant cruising speed (V_o). See equation (5) to get the relationships between V_θ, V_o, a, R_{max} and θ.*

Crisp, 1983); which coincides with the mean range of R max computed for the chemical active space (Table 1). This is probably indirect evidence that the flow field in feeding copepods is used to sense preys at a distance and to detect approaching particles. In any case, the range of this remote sensing chemical detection probably does not exceed the dimensions listed in Table 1; the limitation being mainly related to fluid dynamic at low Reynolds' number.

Table 1. *Range of the radius (R max) of the chemical active space computed from equation (3) related to the concentration (Q) of amino acids released by phytoplankton and the sensory threshold (K) of zooplankton (Values of K are borrowed from Fuzessery and Childress, 1975; Poulet and Ouellet 1982).*

	K (mole)			
	10^{-8}	10^{-6}	10^{-5}	10^{-2}
Q ($\text{mole.cm}^{-3} \times 10^{-6}$)	R_{max} (cm)			
0.3	1.06	0.22	0.05	0.005
1	1.58	0.34	0.07	0.007
2	1.99	0.43	0.09	0.009
5	2.70	0.58	0.12	0.01

After having explored the relationships between Q, R, K and Zp in the chemosensory model with reference to amino acids, we now can question how long it takes a copepod to catch the algae. Each particle, or molecule approaching the active space is moved within the stream field created by the motion of the feeding appendages towards the feeding chamber (Alcaraz et al., 1980; Koehl and Strickler, 1981; Strickler, 1982). Price et al. (1980) and Yule and Crisp (1983) have shown that there is a noticeable change in the beat frequency of the mandibular palps of copepods when phytoplankton is added into the water. At the mean time, copepods swim at a regular speed creating a flow field around the body (Strickler, 1982). Each molecule carried by the fluid is practically stationary in its frame of reference. In order to reach the chemoreceptors, molecules must cross this layer by diffusion (Berg and Purcell, 1977). The flow around the copepods is the Stoke's velocity field described by equation (5) as given by Berg and Purcell (1977):

(5)

$$V = V_o \sin\theta \left(1 - \frac{3a}{4R} - \frac{a}{4R^3}\right)$$

Figure 5 shows the flow field and direction of flow around a copepod swimming at constant velocity (Vo; i.e. cruising speed) through the viscous fluid. The flow field is doubly sheared on the sides of the copepod with velocity (V) changing with θ. Let be $V_o = 0.5\ \text{cm.s}^{-1}$ the average cruising velocity of copepods, as before, $a = 0.1$ cm the radius of a copepod equivalent to a sphere and $0.5 < R < 2.7$ (cm) being the active space radius (Table 1). From the anterior end to the lateral region, the water layer in contact with the copepod surface has a velocity increasing from $0.007\ \text{cm.s}^{-1}$ to $0.3\ \text{cm.s}^{-1}$, depending on the angle θ, taking $1^\circ < \theta < 45^\circ$. Because some sort of contact between the stimulatory molecules and chemoreceptors must be achieved in order to trigger the sensory response of copepods (Laverack, 1974), molecules must traveled the distance comprised between the water layers and the surface of the receptors (Fig. 5). Under such conditions, transport by diffusion must be more effective than advection. According to Berg and Purcell (1977), transport by advection is characterized by the velocity V and by its distance of travel L which determine a time $t_s = L/V_\theta$. Transport by diffusion over a distance L is characterized by a time $t_D = L^2/D$ where D is the diffusion coefficient. Molecules will reach the chemoreceptors by diffusion, when $t_D < t_s$, only if $L < D/V_\theta$. Depending on the angle θ (1° to 45°), with $0.008\ cm.s^{-1} < V_\theta < 0.3\ cm.s^{-1}$ and with $D = 10^{-5}\ cm^2.s^{-1}$ (i.e. amino acids) we get the values for L ($0.3\ \mu m < L < 12\ \mu m$) and t_D ($0.001\ s < t_D < 0.15\ s$). These results mean that at a distance less than 12 µm from the chemoreceptors, copepods have 1 to 150 microseconds to get warning of amino acids released by approaching phytoplankton cells located in the active space. Are these values relevant to the real world? In fact, carnivorous copepods are able to detect, attack and avoid other plankters in a few microseconds, combined with behavioral swimming manoeuvers (Kerfoot, 1978; Kerfoot et al., 1980). Cowles and Strickler (1983) also have reported that the particle capture sequence by filter-feeding copepods requires less than 14 microseconds.

Capture of particles is not always followed by ingestion. Copepods are known to reject particles after capture has been achieved. Particles are either rejected in whole or after being broken down into smaller pieces (Poulet and Marsot, 1978, 1980; Donaghay and Small, 1979; Huntley, 1982; Price et al., 1983). Thus, the complete feeding sequence starts with particle capture, after chemical warning, is followed by particle selection and it ends either by ingestion or rejection of the particle. The way copepods achieve this type of close distance selection is as yet unknown. It is probably under the dependence of chemoreception operating on the feeding appendages in contact with the particles; and, it is likely related both to the surface chemistry (Gerritsen and Porter, 1982) and to the internal chemistry of the cells after mandibular teeths have broken up the cells. We found that intracellular concentrations of dissolved free amino acids were 10 to 100 times higher than the concentrations in water surrounding naturally occurring particles (Poulet, unpublished). Such a high chemical concentration may trigger an intense and fast reflex-reaction, as shown earlier by Poulet and Ouellet (1982), Price et al. (1983).

II. THE ASSIMILATION MODEL

The growth of copepods results from the difference between anabolic and catabolic metabolisms, which is expressed by the general equation for growth rate (G) (i.e. Conover, 1978) as: (6) $G = A - R$, where A and R represent the assimilation and respiration/excretion rates, respectively. Copepods are not completely efficient at assimilating ingested food (Conover and Huntley, 1980); thus, the rate of assimilation can be given by (7) $A = I \, . \, a$, where I is the ingestion rate and a is the absorption efficiency (i.e. assimilation yield). On the other hand, the relationship between ingestion rate and food concentration (P) given by Ivlev (1961) is:

(8) $I = I_{max}\ (1 - e^{-kP})$, where I_{max} is the maximum ingestion rate, k is the slope of the curve. Let simply rewrite equation (8) by

(9) $I = I_{max}.f(P)$ and incorporate this expression with A given by equation (7) into equation (6) which thus, becomes:

(10) $G = I_{max}.f(P).a-R$.

From (10), growth can be related to both ingestion rate, food concentration and assimilation in the positive section of the equation. At that stage, R will be ignored in our discussion. Our approach may look like an over simplification of a complex reality. Nevertheless, the concept that growth of copepods could be induced simply by external factors (i.e. food and temperature levels: McLaren, 1963; Harris and Paffenhöfer, 1976; Conover and Huntley, 1980) is not new. What we outline in the physiological model shown in Figures 1 B, 2 and equation (10) is the fact that internal factors (i.e. assimilation, thus, digestive enzyme activity) could be complementary of the external factors. Vidal (1980) has demonstrated that the growth rate of young copepod stages fed at high food levels (1.5 to 4 ppm) was more strongly influenced by temperature than by food availability, but that of older stages was more dependent on food concentration than on temperature. However, at low food concentrations (less than 2 ppm for *Calanus* and less than 1 ppm for *Pseudocalanus*) growth rates of each copepod species were almost identical (15-20 %) and exclusively food dependent, whatever the developmental stages were. As the growth of copepods becomes temperature dependent when they are not food limited (McLaren and Corkett, 1981), the results from Vidal (1980) suggest that the food requirements are not the same for all stages and species of copepods. Thus, it is necessary, in modeling the growth, to consider the variations of (I) with respect ot the external factors, but internal factors as the digestive enzymes levels and the variations of copepods' requirements also have to be considered.

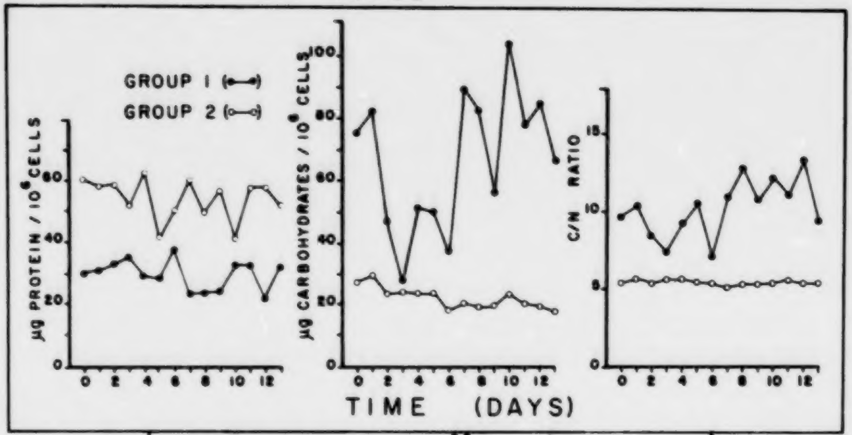
What are the relationships between external and internal factors?

The Ivlev's equation (8) describes ingestion as directly related to a single trophic characteristic (i.e. concentration of food). In reality, I_{max} is also related to some internal factors as well, such as the size of copepods, the nutritional state as illustrated for pre-starved animals (McMahon and Rigler, 1965; Frost 1972). The size of the particulate matter is also known to influence ingestion rate (Frost, 1972) leading to a same maximum carbon ingestion suggesting an internal regulation. The temperature effect on metabolic rates is well known and as Kremer and Nixon (1978) suggested, "a good working hypothesis is that the temperature response will follow an exponential relation according to the Vant' Hof rule". Petipa (1966) and Smayda (1973) showed the relationships between temperature and I_{max} for fully fed *Acartia*. But under natural food conditions, no significant temperature effect on ingestion is found within the temperature range faced by copepods during their life cycle ($\Delta\theta^{\circ} < 12^{\circ}C$) (Poulet, 1974; Conover and Huntley, 1980). Thus, depending on the food conditions (i.e. limiting or non-limiting for requirements) ingestion is not always temperature dependent.

Is the biochemistry of food of importance? The growth stage of phytoplankton cultures has an influence on ingestion rate of *Daphnia*, suggesting some sort of food selection (McMahon and Rigler, 1965). Recent findings on copepods digestive enzyme activity have shown the role of the concentration and chemical composition of the food on the enzymatic responses (Boucher et al., 1975; Mayzaud and Poulet, 1978; Cox, 1981, Head and Conover, 1983). But the direct link between growth and the internal factors (Fig. 1 B, Fig. 2) has not yet been established for copepods. We have partially verified this model for the brine shrimp *Artemia salina* (Samain et al., 1981).

Two groups of *Artemia* maintained under constant temperature and light conditions were fed during 10 days with two different cultures of *Tetraselmis suecica* (150×10^{6} cells.L^{-1}) which had not the same intracellular chemical concentrations in terms of proteins, carbohydrates and C/N ratio (Fig. 6). The differential chemical composition of the cells was obtained by varying the level of nutrients in the culture medium. Cells of phytoplankton cultivated under low nutrient concentration were protein poor, carbohydrates rich and presented the highest C/N ratio (Group 1 : Fig. 6), whereas it was the opposite for the cells cultivated unter high nutrient concentration (Group 2 : Fig. 6). The ingestion of

FIG. 6



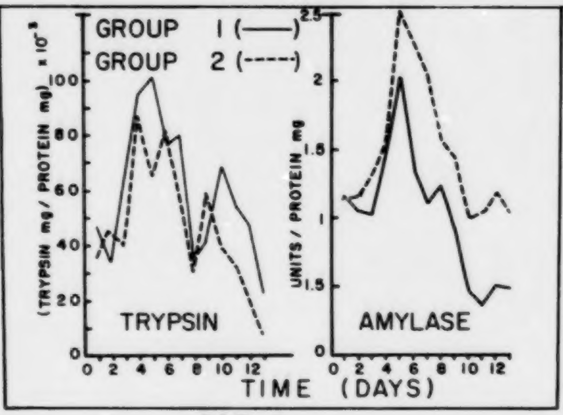


FIG. 7

Figure 6. *Variations of the chemical composition of the cells of Tetraselmis suecica cultivated under two nutrient conditions and offered as food to Artemia during the 13 days feeding and growth experiments (Group 2: cells cultivated with 2.5 folds the normal nutrient concentration; Group 1: cells cultivated with normal nutrient concentration of the Conway medium).*

Figure 7. *Responses of the specific digestive enzyme activity (trypsin and amylase) of Artemia salina fed on two chemically different food regimes (Groups 1 and 2: Same as in Figure* **6** *and Table 2). (From Samain et al., 1981). Number of observations for each specific enzyme and each group is N = 26.*

Artemia was different according to the type of food provided. Even though the cell concentrations were identical in the two sets of feeding experiments, Artemia preferentially consumed Tetraselmis in group 1 at rates higher than in group 2 (Table 2). However, due to the differential chemical composition of the cells in each group, the protein uptake was similar in both groups, whereas the carbohydrate uptake in group 1 was much higher than in group 2 (Table 2). Different food uptakes are normally expected to lead to differential growth rates among crustacean zooplankton. However, under the specific conditions established in our experiments (Fig. 6) it appears that the growth rate of Artemia was identical even though the quantity of cells ingested was different in each group (Table 2). These results suggest that ingestion rates were modified mainly by the nutritive quality of the food (Fig. 6; Table 2).

Table 2. *Average quantity of cells, proteins and carbohydrates ingested by Artemia fed on Tetraselmis suecica presenting different chemical composition and mean growth rate of Artemia. Groups 1 and 2: same as in Figures 6 and 7. Duration of the experiment: 13 days from nauplii to adult stages in 20 L tanks at 22^{o}C. N: number of observations in each group.*

Type of food	**Ingestion rate**			**Growth rate**
	Number of cells (10^6cel.mg Prot.$^{-1}$H^{-1})	**Protein** (µg.mg Prot.$^{-1}$H^{-1})	**Carbohydrates** (µg.mg Prot.$^{-1}$H^{-1})	(mm.Day^{-1})
Group 1	1.9	54.8	128	0.092
Group 2	1.0	54.9	23.2	0.103
	N=9	N=9	N=9	N=11

One way to understand the type of regulation of ingestion by the chemical quality of food is to postulate that ingestion is under the control of chemoreception (Fig. 2). A growing number of experimental results on copepods tend to support this contention (Poulet and Marsot, 1978, 1980; Donaghay and Small, 1979; Huntley, 1982; Fiedler, 1982). We also need to assume that digestive enzyme concentration must change with the qualitative variations of the ingested food, so that assimilation is stabilised. Equal growth rates (Table 2) can be explained only if a fraction of the ingested food is assimilated by Artemia. We have shown that stable uptake of proteins induced stable response in terms of specific trypsin activity of Artemia. Conversely, differential ingestion of carbohydrates could be balanced by significant differences in the specific activity of amylase (Fig. 7). The more carbohydrates ingested the less active was the amylase, depending on the chemical properties of the Tetraselmis cells (Figs. 6 and 7; Table 2). Using equation

(11) $A = \frac{A_{max} \cdot E.I}{K + I}$ and (12) $\frac{A}{I} = \frac{Amax.\ E}{K + I}$

proposed by Samain et al. (1980), where A is the assimilation rate, E the digestive enzyme concentration, I the ingestion rate and K is a constant, we understand why the levels of assimilated proteins and carbohydrates are similar in each experimental group (Figs. 6 and 7; Table 2). Digestive enzymes' concentrations can balance qualitative and quantitative differences existing in the ingested food, so that assimilation is maintained at a constant level and leads to the same optimum growth rate (i.e. equation (6) and (10), Table 2 and Fig. 7). Following the same line of reasoning, growth rate could be constant, under various food regimes only if digestive enzymes were acclimated to the types of food encountered by filter-feeders. It is likely that the variability of the enzyme activity often reported for copepods under variable food conditions do just this (Mayzaud and Poulet, 1978; Moal et al., 1981; Cox, 1981; Baars and Oosterhuis, 1984). Results in Figures 6 and 7, and Table 2, are the first reports simultaneously relating the quality of food to ingestion rate, enzyme activity and growth of crustacean zooplankton that support our physiological model (Fig. 1B; Fig.2).

Equation (11) suggests that the digestive enzymes should decrease when the ingestion increases, or reverse, in order to maintain constant assimilation, probably at the level of the needs, leading to a negative correlation between digestive enzymes and food. Such a negative correlation have been recorded under field conditions by Boucher et al. (1975), Samain et al. (1983) for amylase and trypsin activities, by Cox (1981) for laminarinase and by Hasset and Landry (1982) for other carbohydrases. According to equation (12), the assimilation yield (A/I) is decreasing when ingestion of food is higher than the needs. But positive correlations between digestive enzymes and food are also reported by Boucher and Samain (1974), Mayzaud and Poulet (1978), Samain et al. (1983). According to equation (12) in the case food is limiting, the assimilation yield can be optimized when the digestive enzymes levels and the ingestion vary the same way. Furthermore, the data from Van Wormhoudt (1982) clearly demonstrated such a regulation between food quality and enzyme activity of the shrimp _Palaemon serratus_.

Looking back at the food concentration and the requirements for growth of the copepods, two different schemes should be considered:

- 1 - When food is limited: chemosensory mechanisms are probably of importance to allow copepods to find their food resources. According to equations (9) and (11), I is then related to P, I_{max} is depending on internal factors (McMahon and Rigler, 1965; Frost, 1972) and assimilation yield (A/I) is probably maximum. In the case, growth is food dependent as shown by Vidal (1980).

- 2 - When food is not limited: growth is temperature dependent (i.e. Vidal, 1980). Thus, chemoreception, ingestion rate and digestive enzyme activity may not be the crucial factors; simply because saturation or "plateau phase" is reached (i.e. Frost, 1972, 1977).

Our discussion has illustrated the need for additional information on the mechanisms permitting transformation of organic matter, not simply in terms of energy, but rather in terms of biological and physiological processes which allow copepods to adjust their growth requirements to food stocks.

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CONSTRAINTS ON THE EVOLUTION OF COPEPOD BODY SIZE

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Abstract: Using a model based on the theory of adaptation, Myers and Runge (1983; this volume) hypothesize that a seasonal increase in mortality rates causes the well known inverse relationship between temperature and body size observed for multivoltine planktonic copepods. The model in its present form would be invalid, however, if genetic variability to change the development time-temperature relationship does not exist; in other words, if, for individual growth rates observed in the field, body size is physiologically or thermodynamically constrained to be smaller at higher temperatures. Seasonal variation in food supply may also influence body size, but does not fundamentally alter predictions of the theory of adaptation unless individual growth rates in natural populations decrease with seasonal increases in temperature. Testing of the theory of adaptation and its alternatives would clarify over understanding of the coupling between temperature, growth, and mortality in planktonic copepods and perhaps in ectotherms generally.

INTRODUCTION

Except in boreal regions, planktonic copepods usually pass through two or more generations annually. It is a general observation that body length of adult copepods is inversely related to the temperature during development, so that, in temperate climates with a seasonal temperature variation, each generation of the annual cycle is successively smaller (e.g. Deevey, 1960; McLaren, 1963).

What are the underlying reasons for seasonal variations in body size? According to the theory of adaptation discussed by Myers and Runge (1983; this volume), the final body size of copepods growing at a higher rate at warmer temperatures should be larger than that of counterparts developing at cooler temperatures, all other factors being the same. That the opposite relationship is generally observed in nature implies that mortality rates must be increasing with temperature at a rate equal to or faster than growth rate, for the observed body size to be adaptive (Myers and Runge, 1983; this volume).

In this paper, we examine two other explanations of seasonal variation in copepod body size. First, the physiological constraint hypothesis states that genetic variability for changes in final body size as a function of temperature may be nonexistent, due to physiological of thermodynamic limitations on growth and development. Second, the food limitation hypothesis states that seasonal changes in food availability generally limit copepod growth rates, resulting in smaller body sizes at higher temperatures. These explanations are discussed in the context of the evolutionary model, as they do not necessarily exclude an adaptive interpretation.

Copepods attain a terminal body size (certainly in length; we will assume in weight also, although there is evidence that this is not strictly the case) upon reaching sexual maturity. Thus, final size is the consequence of the developmental rate, which controls how fast the copepod molts through its developmental stages, and the growth rate, which controls how much weight or body length is incremented at each molt.

PHYSIOLOGICAL CONSTRAINTS

If growth rates and development rates have different functional relationships with temperature, adult body size will be smaller or larger at warmer developmental temperatures, depending on which of the two processes increases more as temperature increases. In planktonic copepods, growth rates generally have smaller temperature coefficients than development rates, hence body size are smaller. This has been discussed by McLaren (1963) and by Miller et al. (1977; see their fig. 8) who put the situation succinctly: "If an animal is forced through its fixed quota of molts quickly by high temperature, it simply has no chance to grow large".

This physiological relationship may be adaptive (as discussed by Myers and Runge in this volume) or it may be due to a physiological constraint. This distinction is usually not made explicit in analyses of body size, even though very difficult biological conclusions are implied by the two alternatives. By "constraint" we mean a fundamental physiological, biochemical, or thermodynamic barrier that limits the possible shapes of the development rate-temperature relationship. In quantitative genetic terms this implies that there is no additive variation for a shift in this relationship to allow body size to be larger at higher temperatures. Without genetic variation, it would be impossible to select a population with body sizes larger at higher temperatures in conditions of excess food.

The nature of the development time-temperature relationship is of particular importance in the evolutionary model. In predicting mortality rates needed to make the observed life-history characteristics adaptive, the age at sexual maturity is allowed to vary freely to determine the body size that gives the maximum fitness under a given mortality regime. If for any temperature copepod development time is constrained to be a certain value, then the model we presented for Acartia clausi (Myers and Runge, 1983) would be invalid.

Experimental evidence suggests that development of copepods may be the consequence of a series of biochemical reactions which are entirely rate-regulated by temperature in the presence of excess food. Landry (1975a) found that development rates of Acartia clausi fed excess food are predictable from egg development times of the species. This result corroborated a conclusion made earlier by Corkett and McLaren (1970), based on their studies of species of Pseudocalanus, Eurytemora, Temora, and Acartia. Furthermore, Landry (1975b) showed that the relationship of relative egg development times to temperature is the same for 9 species of marine, planktonic copepods. These data suggest that a similar process is controlling the shape of the development time-temperature function.

The question of interest here is the extent to which the temperature relationship of development is genetically variable. Sharpe and Mitchele (1977) presented a model of poikilotherm development determined by activation and inactivation of control enzyme systems, coupled with thermodynamic characteristics of the enzyme reaction rates. Their analysis allows for considerable variation in both shape and translation of the rate-temperature curve, depending on the extent of inactivation of enzyme systems, for which there is potentially additive genetic variation. Clarke (1983) presents the evidence for considerable temperature compensation in the development characteristics of different copepod species, although seasonal variation within a population is not specifically discussed. Perhaps the strongest evidence against a physiological constraint operating generally in ectotherms is that multivoltine insects generally mature of a larger size at higher temperatures (reviewed in Myers, 1983), an observation that is consistent with the hypothesis of adaptation but not with the hypothesis of constraint.

The critical experiment to determine the extent of genetic variability has not been carried out. Conditions required for a proper test of a physiological constraint have been discussed by Myers (1983). There is in addition the possibility that, while additive variation for a shift in the development time-temperature relationship exists, the shift is coupled with detrimental pleiotropic effects and so is not expressed (Myers, 1983). This alternative could also be disproved by the appropriate experiment in quantitative genetic selection.

It is important to note that constraints on maximum and minimum size of a species may be in effect regardless of constraints on the development time-temperature relationship postulated here. For example, Corkett and McLaren (1978) found that, in populations in Pseudocalanus from the Canadian Arctic, Long Island Sound, and Loch Striven, minimum and maximum adult body sizes were similar even though they occurred at very different developmental temperatures. As copepods appear to have fixed cell numbers (McLaren and Marcogliese, 1983), the range of possible body sizes may be related to constraints on nuclear size and DNA content (Cavalier-Smith, 1978).

FOOD LIMITATION

In laboratory experiments, Vidal (1980) and Klein Breteler and Gonzalez (1982) have shown that food shortage can limit final size of copepods, in terms of both weight and length. There is growing evidence that food availability may limit growth and reproduction in natural copepod populations (eg. Landry, 1978; Checkley, 1980; Durbin et al., 1983; Runge, in press). As phytoplankton food and temperature are often negatively correlated in temperate, oceanic environments, food limitation may be as important as temperature in determining seasonal variation in final body size (Deevey, 1960; Frost, 1974; Vidal, 1980; Klein Breteler and Gonzalez, 1982).

While food availability can influence final body size of copepods, we question whether food limitation by itself is ever a sufficient explanation of the inverse body size - temperature relationship. In laboratory experiments under, constant food conditions, body size of copepods was still either negatively related to temperature (Coker, 1938; Corkett and McLaren, 1978; Landry, 1978; Vidal, 1980) or, at best, remained unchanged (Mullin and Brooks, 1970a,b). In most cases, therefore, food limitation apparently would only determine the extent to which body size is lower at higher temperatures. We suggest that food effects be divided into 3 categories, as follows:

(1) Food limitation occurs especially at higher temperatures but individual growth rates in natural populations still generally increase as ambient temperature rises. In this situation, mortality rate is still predicted to increase with temperature, given the inverse body size relationship. For example, while growth of Acartia clausi in Jakles Lagoon appears to have been food limited in the late summer (Landry, 1978), growth rates nevertheless still increased with temperature (Fig. 14: Landry, 1978); hence predicted and observed mortality rates were also higher. Here, food limitation is not an explanation and the probable cause is the constraint hypothesis or the adaptational theory suggested by Myers and Runge (this volume).

(2) Food limitation at higher temperatures is so severe that individual growth rates generally decrease with seasonal increases in temperature. In this case, the prime requirement needed for the application of the theory in Myers and Runge (this volume) is violated and sexual maturity would occur

at smaller sizes at higher temperatures with a temperature-independent mortality regime. It is unlikely that this is a general situation, but it may occur during stratified summertime conditions for larger copepods, like species of Calanus, adapted to exploit phytoplankton blooms (Vidal, 1980).

(3) Food is generally limiting during colder ambient temperatures and body size is greater at higher temperatures, in exception to the general rule. We are not aware of many published examples of this situation. Evans (1981) found no evidence for a simple size-temperature relationship for Temora longicornis and concluded that variability in food supply was the overriding factor determining body size of the species in the North Sea.

CONCLUDING REMARKS

The existence of either physiological constraint or food effects discussed here has important consequences for understanding the ecology or physiology of copepods. If a physiological constraint is involved, then there is something fundamental about the biology of copepods, and perhaps ectotherms in general, that we do not understand. On the other hand, support for the hypothesis of adaptation of Myers and Runge (1983; this volume) implies a general coupling between temperature, growth and mortality and advances the use of life-history theory to estimate mortality rates of natural populations.

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DISTRIBUTION AND ECOLOGY OF CLETODIDAE (CRUSTACEA, COPEPODA) AT THE ICELAND-FAROE RIDGE FROM 290 m to 2500 m WATER DEPTH

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Abstract: There are only few informations about the Harpacticoida from the off-shore cold water areas. The investigations on the deep sea Harpacticoida from the Iceland-Faroe Ridge have shown exclusively species new to science except of 11 among the Cletodidae. Based on the taxonomic determination notes on the ecology and distribution of the species are presented. 31.0% of the collected specimens belong to the Cletodidae and were found to represent 44 different species belonging to 11 genera. The hydrographic conditions on the Arctic Sea Slope are more stable than on the North-Atlantic Slope and the sediments here are coarser. Based on this conditions the Arctic Sea Slope presents a higher species diversity.

INTRODUCTION

Although there is a lot of information on the ecology and distribution of the macro- and meiofauna from the deep sea (Bowman, 1971; Coull, 1971; Coull et al., 1977; Dinet, 1979; Gerlach, 1971; Gray, 1981; Hessler and Sanders, 1967; Slobodkin and Sanders, 1969; Thiel, 1971, 1972, 1982), not much is known about deep sea Harpacticoida. Seven papers in all (Coull, 1971, 1972; Hartzband and Hummon, 1974; Montagna and Carey 1978; and Thistle, 1977, 1978, 1979) deal with the ecology and distribution of deep sea harpacticoids. Numerous other papers are devoted to the description of new species (Becker, 1972, 1974; Becker et al., 1979; Bodin, 1968; Brotzky, 1963; Itô, 1980, 1983; Montagna, 1980; Smirnov, 1946; Soyer, 1970) and include some information on the localities where the species have been found. Within the last four years first reports have been published on the influence of sediment characters and disturbation on the distribution of harpacticoids in the benthos (Sherman and Coull, 1980; Thistle, 1980; Ravenel et Thistle, 1981). A review article by Hicks and Coull (1983) on the ecology of marine meiobenthic harpacticoid copepods has recently appeared as well as a thorough treatment by Arlt (1983) of the taxonomy and ecology of some harpacticoids in the Baltic Sea and the Kattegat.

The present paper deals with the deep sea Harpacticoida from the Iceland-Faroe Ridge, collected by Hj. Thiel, University of Hamburg and deposited at the Zoologisches Museum Kiel. These harpacticoids have been investigated under taxonomical and ecological aspects. First determinations of the material have shown that most of them belong to new species of which 35 along with one new genus have already been described (Schriever, 1982a,b, 1983, 1984, in press). Further new species of the genera Paranannopus, Cylindronannopus, Eurycletodes and Mesocletodes are in press and additional new species of various cletodid genera will be published in a subsequent paper.

MATERIAL AND METHODS

The results presented here are based on a series of 28 samples taken on cruise 98 of F.R.V. "Anton Dohrn" in 1966 crossing the Iceland-Faroe Ridge. This series started at a depth of 2500 m in the Atlantic Ocean and reached over the summit of the ridge down to a depth of 1825 m in the Norwegian Sea. The locations are illustrated in Figure 1 and listed in Table 1. Details about the cruise, the samples and the distribution of the meiofauna are given by Thiel (1971). The copepods were counted and fixed in 4% formalin. They were dissected and determined with the aid of a Wild M8 Binocular and a Wild M40 Microscope.

Table 1. *Stations of F.R.V. "Anton Dohrn", cruise 98, 1966*

Station	Position	Depth	Date
481	60°46'N - 16°06'W	2500 m	09. July 1966
480	61°34'N - 14°46'W	2000 m	08. July 1966
483	61°42'N - 14°10'W	1805 m	10. July 1966
479	62°04'N - 13°56'W	1555 m	06. July 1966
477	62°34'N - 13°01'W	1015 m	06. July 1966
475	62°52'N - 12°23'W	610 m	06. July 1966
474	62°57'N - 12°08'W	505 m	05. July 1966
468	63°33'N - 11°40'N	364 m	05. July 1966
467	63°31'N - 11°15'W	295 m	04. July 1966
486	63°14'N - 11°37'W	435 m	16. July 1966
464	63°31'N - 10°11'W	500 m	04. July 1966
510	63°38'N - 09°48'W	600 m	24. July 1966
492	63°06'N - 07°25'W	985 m	21. July 1966
462	63°30'N - 07°34'W	1000 m	02. July 1966
461	63°26'N - 06°32'W	1510 m	01. July 1966
487	63°29'N - 06°32'W	1510 m	17. July 1966
491	63°06'N - 06°27'W	1540 m	20. July 1966
490	63°04'N - 06°05'W	1685 m	19. July 1966
489	63°30'N - 05°55'W	1825 m	18. July 1966

RESULTS

The determination showed that out of 858 specimens altogether 31,0 % (266 specimens) belong to the family Cletodidae. They were found to represent 44 different species belonging to 11 genera. 31 of the 266 specimens (11,7%) could only be identified as cletodids or cletodid copepodids (see Table 2) and

SPECIES LIST

- *Cletodes* Brady, 1872
  - *Cletodes endopodita* (Schriever, 1984)*

- *Heteropsyllus* T. Scott,1894
  - *Heteropsyllus serratus* Schriever, 1983
  - *Heteropsyllus* sp. 1
  - *Heteropsyllus* sp. 2
  - *Heteropsyllus* sp. 3

- *Mesocletodes* Sars, 1909
  - *Mesocletodes irrasus* T. and A. Scott, 1894
  - *Mesocletodes parabodini* Schriever, 1983
  - *Mesocletodes variabilis* Schriever, 1983
  - *Mesocletodes trisetosa* Schriever, 1983
  - *Mesocletodes duosetosus* Schriever in press
  - *Mesocletodes thieli* Schriever in press
  - *Mesocletodes faroerensis* Schriever in press
  - *Mesocletodes kunzi* Schriever in press
  - *Mesocletodes quadrispinosa* Schriever in press
  - *Mesocletodes* sp.
  - *Mesocletodes* Copepodids

- *Eurycletodes* Sars, 1909
  - *Eurycletodes monardi* Smirnov, 1946
  - *Eurycletodes gorbunovi* Smirnov, 1946
  - *Eurycletodes* aff. *oblongus* Sars, 1920
  - *Eurycletodes* aff. *latus* (T. Scott, 1892)
  - *Eurycletodes quadrispinosa* Schriever in press

- *Hemimesochra* Sars, 1920
  - *Hemimesochra trisetosa* Coull, 1973
  - *Hemimesochra* sp. 1
  - *Hemimesochra* sp. 2
  - *Hemimesochra* sp. 3
  - *Hemimesochra* sp.

- *Stylicletodes* Lang, 1936
  - *Stylicletodes longicaudatus* (Brady and Robertson, 1880)

- *Monocletodes* Lang, 1936
  - *Monocletodes varians* Lang, 1936*

- *Paranannopus* Lang, 1936
  - *Paranannopus langi* Wells, 1965
  - *Paranannopus plumosus* Schriever, 1983
  - *Paranannopus denticulatus* Schriever in press
  - *Paranannopus trisetosus* Schriever in press
  - *Paranannopus singulosetosus* Schriever in press
  - *Paranannopus uniarticulatus* Schriever in press
  - *Paranannopus variabilis* Schriever in press
  - *Paranannopus kunzi* Schriever in press
  - *Paranannopus hicksi* Schriever in press
  - *Paranannopus* sp.
  - *Paranannopus* Copepodids

- *Metahuntemannia* Smirnov, 1946
  - *Metahuntemannia drzycimskii* Soyer, 1970
  - *Metahuntemannia pseudomagniceps* Schriever 1983
  - *Metahuntemannia atlantica* Schriever, 1983
  - *Metahuntemannia triarticulata* Schriever, 1984
  - *Metahuntemannia arctica* Schriever, 1984
  - *Metahuntemannia bifida* Schriever, 1984
  - *Metahuntemannia* Copepodids

- *Cylindronannopus* Coull, 1973
  - *Cylindronannopus bispinosus* Schriever in press

- *Cletodidae* sp. and undetermined *Cletodidae* Copepodids

* = These species were originally described as *Thieliella northatlantica* Schriever 1982 and *Th. endopodita* Schriever 1984. A revision of the genus *Thieliella* is in press (Schriever in press).

Table 2. *The distribution of genera, species and specimens at the slopes and the crest of the Iceland-Faroe Ridge.*

Station	481	480	483	479	477	475	474	468	467	486	464	510	492	462	461	487	491	490	489
Depth in m	2500	2000	1805	1555	1015	610	505	364	295	435	500	600	985	1000	1510	1510	1540	1685	1825
Species																			
Cletodes Brady, 1872																			
Cletodes endopodita								5	1	12	3	6	1	2					
Heteropsyllus T. Scott, 1894																			
Heteropsyllus serratus								1		2	1								
Heteropsyllus sp. 1																	2	1	2
Heteropsyllus sp. 2													1				2		
Heteropsyllus sp. 3																		2	1
Mesocletodes Sars, 1909																			
Mesocletodes irrasus																	1		
Mesocletodes parabodini											1	2							
Mesocletodes variabilis											1		3						
Mesocletodes trisetosa											1								
Mesocletodes duosetosus											1		3	1					
Mesocletodes thieli				1									21						
Mesocletodes faroerensis											1					1	2		
Mesocletodes kunzi																		4	2
Mesocletodes quadrispinosa							2												
Mesocletodes sp.		1	1																
Mesocletodes Copepodites												6	9	1	1				
Eurycletodes Sars, 1909																			
Eurycletodes monardi															1				
Eurycletodes gorbunovi										1									
Eurycletodes aff. oblongus																1			
Eurycletodes aff. latus																	1		
Eurycletodes quadrispinosa	1																		
Hemimesochra Sars, 1920																			
Hemimesochra trisetosa																	1		
Hemimesochra sp. 1																1		1	
Hemimesochra sp. 2																	1	1	1
Hemimesochra sp. 3																			1
Hemimesochra sp.											1								
Stylicletodes Lang, 1936																			
Stylicletodes longicaudatus												1		1					

Table 2 (continued)

Station	481	480	483	479	477	475	474	468	467	486	464	510	492	462	461	487	491	490	489
Depth in m	2500	2000	1805	1555	1015	610	505	364	295	435	500	600	985	1000	1510	1510	1540	1685	1825
Species																			
Monocletodes Lang, 1936																			
Monocletodes varians									1	3	10	5	1	1					
Paranannopus Lang, 1936																			
Paranannopus langi											1		1						
Paranannopus plumosus											1								
Paranannopus denticulatus										1									
Paranannopus trisetosus														1				1	
Paranannopus singulosetosus										1				1					
Paranannopus uniarticulatus				1											1			2	
Paranannopus variabilis																2		1	
Paranannopus kunzi														1					
Paranannopus hicksi																1			
Paranannopus sp.			1																
Paranannopus Copepodids	1			3						2		6	2	4		4		4	
Metahuntemannia Smirnov, 1946																			
Metahuntemannia drzycimskii												1							
Metahuntemannia pseudomagniceps											3		1						
Metahuntemannia atlantica											2		1						
Metahuntemannia triarticulata										1		1							
Metahuntemannia arctica																			1
Metahuntemannia bifida	1												1	1		1		1	
Metahuntemannia Copepodids				1				1	1	1	2	2	1			1		2	1
Cylindronannopus Coull, 1973																			
Cylindronannopus bispinosus				2									4				3		
Cletodidae sp. and undetermined Cletodidae Copepodites	1			4	1			4	6	3		1	7				2	2	

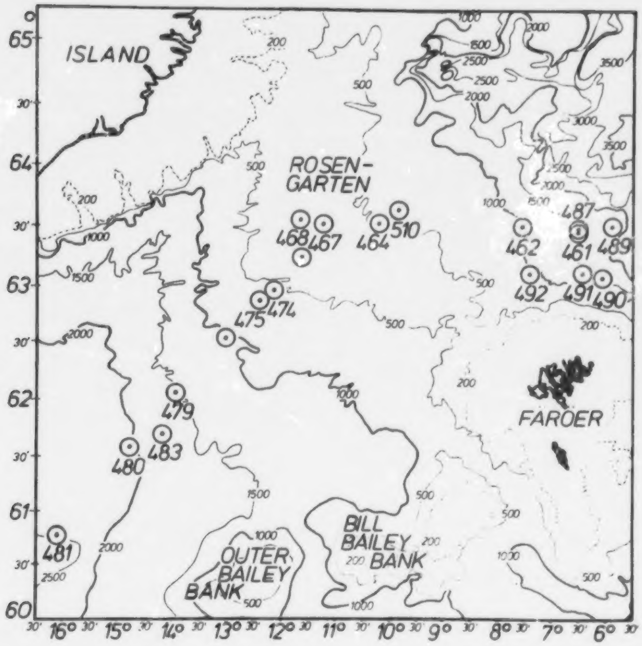
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Figure 1. *Investigation area and stations of F.R.V. "Anton Dohrn", cruise 98, July 1966 (from Thiel, 1971)*

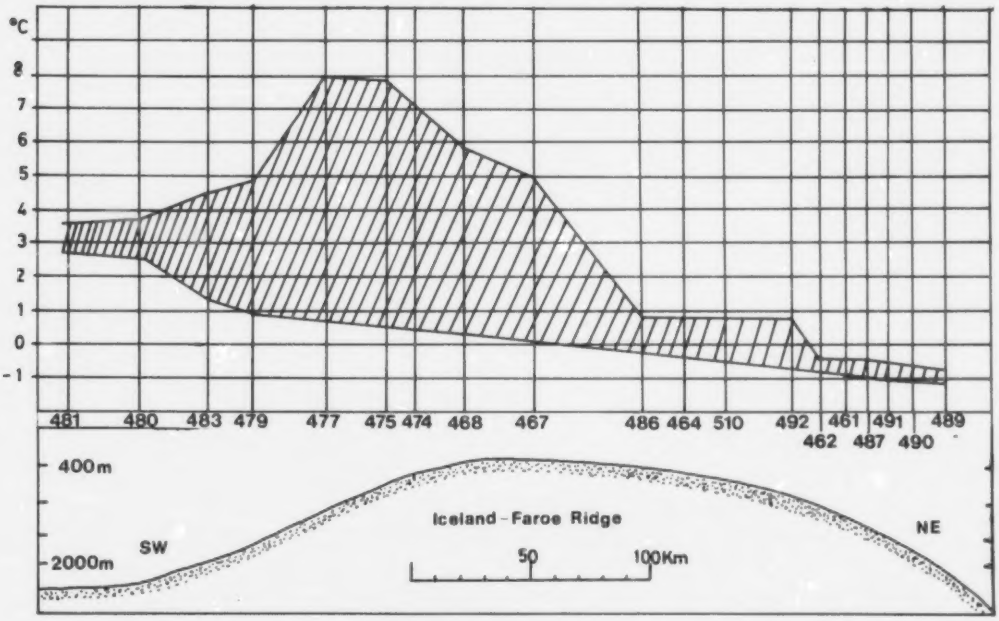

Figure 2. *Temperature fluctuations at the Iceland-Faroe Ridge (from Dietrich, 1956).*

2 specimens of these probably belong to a new cletodid genus which has to be described in a subsequent paper. At the slopes and on the crest the specimens, species and genera were distributed as listed in Table 2. The great difference in the population density and species diversity at the slopes is obvious.

DISCUSSION

The cletodids on both slopes and on the crest of the Iceland-Faroe Ridge vary in density and species diversity as is obvious from Table 2. To understand these differences it is necessary to have a look at the hydrographic and geological conditions in this area. The water temperature fluctuations at the Iceland-Faroe Ridge are shown in Figure 2 (from Dietrich, 1956). Along the Norwegian Sea Slope the temperature is stable at about 0°C down to 800 m depth and decreases to -0,5°C in greater depth; the water current at the sea bottom is weak. Contrary to this very unstable conditions exist on the crest and down the North-Atlantic Slope. From the Norwegian Sea cold bottom water irregularly overflows the crest and streams down the Atlantic Slope. The overflow causes water temperature fluctuations between +1°C and +8°C on the crest and down to 1000 m depth. Beyond this depth the conditions become more stable and the water temperature fluctuation is less than 1°C (Dietrich, 1956).

The strong bottom currents of up to 50 cm/sec (Dietrich, 1960) on the North-Atlantic Slope which are caused by the overflow, disturb the sediments in this area (Jones et al., 1970). Reflection profiles and geophysical measurements (Fleischer et al., 1974, Roberts et al., 1979) show a marked asymetry of sediment distribution across the Ridge, the sediment cover being much thicker and more continuous on the Norwegian Sea Slope. The influence on the sediments is confirmed by the sediment granulometry. The sorting coefficient of 12 sediment samples is presented in Table 3 (from Thiel, 1971). The unstable conditions on the North-Atlantic Slope influence the whole meiofauna (Thiel, 1971). The Norwegian Sea Slope is the richest area (720 ind./cm^2 meiofauna) of the Norwegian Sea (Dinet, 1979). The role of sedimentcharacters on the distribution of harpacticoid copepods is discussed by Ravenel and Thistle (1981).

Table 3: *Sorting Coefficient of 12 samples from the Iceland-Faroe-Ridge*

Station	**Depth**	**Sorting Coefficient**
481	2500 m	3,25
480	2000 m	1,27
483	1805 m	1,84
479	1555 m	1,45
475	610 m	1,83
474	505 m	1,35
467	290 m	1,54
486	435 m	1,58
464	500 m	3,67
492	985 m	2,21
491	1540 m	3,41
490	1685 m	2,84

What applies to the total meiofauna is also reflectecd by the benthic harpacticoids. The so far collected 858 specimens are dominated by 266 specimens of the family Cletodidae. The genera found (Monocletodes, Mesocletodes, Eurycletodes, Hemimesochra, Paranannopus, Metahuntemannia and Cylindronannopus) are the same as those commonly reported from deep sea studies (Smirnov, 1946; Bodin, 1968; Por, 1965, 1967; Soyer, 1970; Becker, 1972; Coull, 1972; and Thistle, 1978). Even though the genera are widely distributed the same species are not found (Coull, 1972). The species list shows that only 10 of the 44 species reported here are known from previous studies (Smirnov, 1946; Coull, 1973). All ten have been described from the North Atlantic Ocean.

The high species diversity and low abundance of Harpacticoida in the deep sea is noted by several authors (Por, 1964, 1967; Bodin, 1968; Soyer, 1970; Coull, 1971, 1973; and Thistle, 1978). This study shows that this is as well true for the family Cletodidae over the Iceland-Faroe Ridge. The role of disturbance (Sherman and Coull, 1980; Thistle, 1978, 1980), here caused by the overflow from the Norwegian Sea, on the benthic Harpacticoida density and abundance (Dayton and Hessler, 1972; Thistle, 1978) is obvious on the crest and at the North Atlantic Slope. Additionally the food conditions on the southern slope are bad for the meiofauna. The sedimentation of organic matter from shallow water layers is low. Here strong currents transport the drop off from the upper layers far south in the Atlantic Ocean and the scarce food supply influences the benthic harpacticoid community.

The results of this study are based on only 28 samples and reflect the conditions in July 1966. The low number of samples is probably not enough to give a real picture of the harpacticoid distribution. Additional samples, taken by Prof. W. Noodt on the same cruise will certainly yield more detailed information, but in all the following conclusions can already by drawn:

- what applies to the total meiofauna of the deep sea, high species diversity and low specimen abundance, is also reflected by the Cletodidae on the Iceland-Faroe Ridge.;
- the distribution of Harpacticoida on the Iceland-Faroe Ridge is influenced by the hydrographic conditions in this area.

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ASPECTS OF CALANOID COPEPOD DISTRIBUTION IN THE UPPER 200 M OF THE CENTRAL AND SOUTHERN SARGASSO SEA IN SPRING 1979

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Abstract: A series of 51 stepped and 2 integrated hauls including night, day, and crepuscular tows (mesh size 0.30 mm) were collected during a four-weeks period in March/April 1979 ("Anton Dohrn" Cruise 92/210) in the Sargasso Sea (latitudes 21 - 32°N, longitudes 55 - 70°W). Structure and taxonomic composition of the calanoid fauna were analysed. Both horizontal and vertical distributions of the prominent species have been studied. Considering abundance or diversity, a marked decline with latitude due to hydrographical conditions was generally observed both among adults and immatures. Average numbers of copepods were almost three times higher in the north than in the south. Peak numbers of species were recorded in the upper 100 m. Of the 101 species of calanoid copepods identified from the upper 200 m, *Lucicutia flavicornis* was most abundant accounting for 18 % of the total number of specimens collected, *Clausocalanus furcatus* and *Ctenocalanus vanus* ranking second and third, respectively.

INTRODUCTION

During the German Sargasso Sea Eel Expedition in spring 1979 mesozooplankton were collected providing data on the local epipelagic fauna. A study of the calanoid copepods proved worthwile, particularly, since information on the central and southern part of the Sargasso Sea is scarce, in contrast to the northern area that is better documented (e.g. Moore, 1949; Grice and Hart, 1962; Deevey, 1971; Deevey and Brooks, 1971, 1977).

The present study reports some results on abundance and taxonomic composition of the calanoid fauna. An extended version will be published elsewhere.

MATERIALS AND METHODS

Samples were collected on cruise 92/210 of R.V. "Anton Dohrn" in the Central and Southern Sargasso Sea between 31°40' - 20°45'N and 69°40' - 55°30'W from 20 March to 15 April 1979 (Fig. 1) using a multiple opening/closing Bé net, modified after Weikert and John (1981). Mesh size was 0.30 mm, average area filtered 0.26 m^2. The net was towed at a speed of 0.7 m/s as near to the vertical as possible. Five standard depth intervals were sampled consecutively during one haul: 0 - 25, 25 - 50, 50 - 100, 100 - 150, 150 - 200 m. Owing to difficulties in exact release of the opening/closing mechanism at desired depth, the actual depth deviated slightly so that in later analyses both near-surface steps were treated as one single, 0 - 50 m catch (see John, 1984). Calculations of abundances have been conducted on the basis of corrected depth levels, however.

A total of 49 complete series of hauls were taken. In two hauls one step each had been lost, and two tows integrated the entire 200 - 0 m water column. Of the total of 51 stepped hauls 27 were taken by day, 17 at night, and 7 were crepuscular tows exclusively taken during dusk hours.

Of a total of 255 samples all were analysed without aliquoting and counts were made on both adult and immature calanoids. Specimens per 200 m haul ranged from 230 to 3,600 constituting 28 to 57 calanoid species.

RESULTS

General abundance. - Disregarding latitudinal or diurnal changes, copepod abundance varied between 4.2 and 62,5 specimens per cubic meter with a mean of 22.2 for the entire study area. Peak abundance for total calanoids per 50-m horizon was 132 m^{-3}. In order to compare samples from different latitudes, the 22^{o} isotherm at 100 m depth was chosen to divide the study area into a more densly populated nothern and a less populated southern area. This temperature was found by Wegner (1982) to mark the southern limit of the subtropical convergence during Cruise 92/210. Moreover, nearly equal numbers of samples could thus be associated with either station group. Resulting mean abundances of copepods are shown in Table 1.

Table 1. *Mean abundance of total calanoid copepods, grouped for temperature zones and light conditions (standard deviation and number of hauls per group are given).*

Temperature (100 m depth)	**Daytime hauls**	**Twilight hauls**	**Night hauls**
< 22^{o} C	$\bar{n}$ m^{-3} = 23.8 s.d. = 9.5 n = 13	$\bar{n}$ m^{-3} = 19.0 s.d. = 6.0 n = 3	$\bar{n}$ m^{-3} = 39.0 s.d. = 19.0 n = 9
> 22^{o} C	$\bar{n}$ m^{-3} = 14.6 s.d. = 5.5 n = 15	$\bar{n}$ m^{-3} = 19.0 s.d. = 1.9 n = 4	$\bar{n}$ m^{-3} = 21.4 s.d. = 2.5 n = 8

Samples from the northern region amounted between 1.6 and 1.8 times higher than southern stations for day and night, respectively. Low abundances for twilight hauls were mainly caused by a relatively southern position of these stations, they are thus not regarded typically for this subregion. Night/day abundance ratios proved nearly identical in both areas, especially regarding immatures (factor of 1.5 in both areas). In the north adults exhibited an increased night/day ratio (1.77 vs 1.42) which might to some extent be caused by a higher percentage of diurnally migrating specimens noted for the genus Pleuromamma in particular. In order to eliminate diurnal differences in abundance and to achieve comparable nighttime values for the whole region, day hauls were corrected by a factor of 1.4

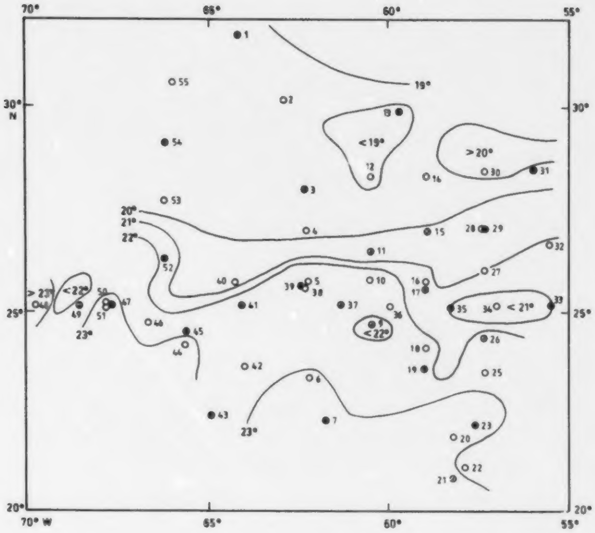
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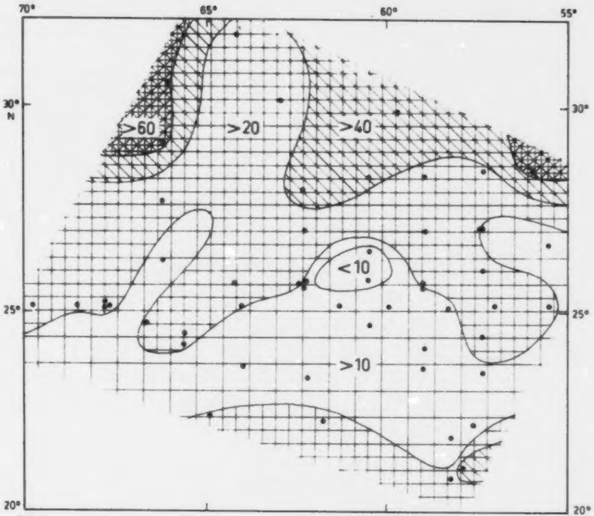
Figure 1. *Study area showing location of stations and isotherms (°C) at 100 m depth during "Anton Dohrn" Cruise 92/210. Open circles represent daytime stations, filled circles are night hauls, and crossed circles indicate twilight samples.*

Figure 2. *Abundance of total calanoid copepods (No. m^{-3}) in the upper 200 m computed for night hauls.*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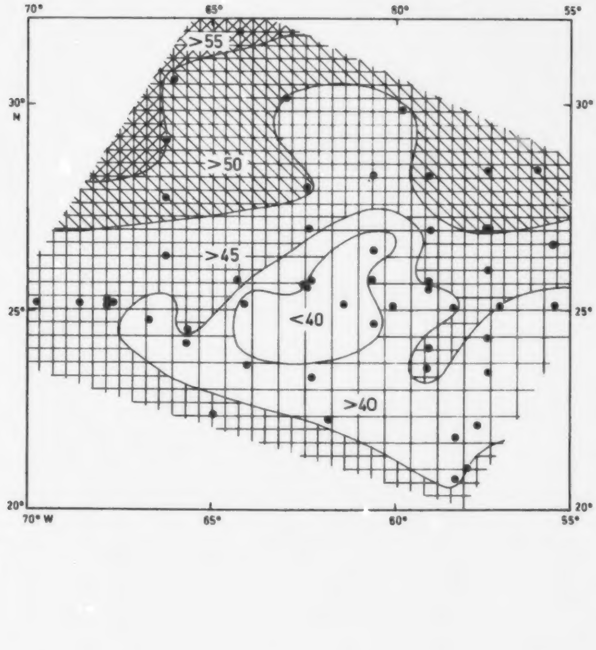
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Figure 4. *Number of calanoid copepod species per 200 m vertical tow, computed for night hauls. Crepuscular hauls not considered.*

considering possible daytime avoidance. Resulting distribution patterns are shown in Fig. 2. Since concentration patterns in adult and immature copepods revealed a striking similarity, only total calanoid abundance is given. Generally, maximum concentrations were found in the north-western and north-eastern area for immatures and adults, respectively. Geostrophic calculations of Wegner (1982) show that both regions were characterized by influx of waters from higher latitudes. Minimum concentrations were limited to lat. 26°N, long. 59 - 62°W in the convergence area centered within the region of very closely spaced 20 to 22.5°C isotherms at 100 m depth constituting a frontal zone. Further south increasingly higher abundances were recorded, particulary regarding adults. Thus, it appears that copepod abundance was negatively correlated with hydrographic conditions in frontal zones. Findings of Colton et al. (1975) suggest that thermal fronts, characterized by near-surface changes of at least 1°C/10 km, can mark faunal boundaries for species like Calocalanus pavoninus or Clausocalanus furcatus. During the present study, however, both species were found on either side of the frontal zone. Regarding copepod abundance in the north and south a general decline by a factor of 2.8 was found when comparing the four latitudinally extreme nighttime stations. This is in close agreement with observations of Backus et al. (1969) dealing with mesopelagic fishes and John (1984) giving a survey on larval fishes from both sides of the convergence area. Besides frontal zones possibly affecting copepod distribution, north/south differences in abundance seem to be clearly related to a high primary production in the north caused by nutrient enrichment of the surface layers during winter mixing and a highly reduced nutrient replacement in southern waters due to permanent thermal stratification (Menzel and Ryther, 1960).

Reported abundance values of copepods from the norhern or southern Sargasso Sea (Calef and Grice, 1967; Deevey and Brooks, 1977; Grice and Hart, 1962) appear to correspond roughly with present data considering different sampling techniques or varying seasons.

Vertical distribution. - Disregarding regional aspects, copepod abundance varied within the four depth layers according to hour of sampling and age structure of the population. Immature calanoids were apparently vertically more evenly distributed than adults, though both decreased in numbers with depth, the lowest level usually containing smallest numbers of individuals. However, values obtained should be treated with considerable caution considering latitudinal and seasonal variations. Based on all stepped hauls, more than three fifth of the adult population were found in the upper 100 m by day (Fig. 3). Night data suggest a significant rise towards upper layers, maximum numbers now occurring in the upper 50 m. Daytime abundance of immatures differed but slightly vertically. During dark hours yet a more pronounced upward trend was indicated. This can just as well be seen by the 50 % level of the entire population located at 81.9 and 71.2 m (adults) or 96.7 and 81.3 m (immatures) for day and night, respectively.

Abundant species. - Table 2 lists the most abundant ten adult and five immature species, respectively. In order to elucidate temperature preferences, a north/south abundance ratio was calculated for each prominent species. Values above 1.65 (general abundance n/s ratio) indicate a more northerly distributional pattern, smaller factors suggest southern predominances of taxa. On average the five most abundant species (both with adults and immatures) contributed about half of the total catch.

Table 2. *Mean abundance and percentage composition of the principal calanoid copepod species (a: adults; b: immatures) of Cruise 92/210, calculated for the upper 200 m. North/south abundance ratio and standard deviation are given.*

	Species	NUMERICAL abundance (No. m^{-3})	s.d.	RELATIVE abundance (%)	N/S-ratio
a)	1. Lucicutia flavicornis	2.13	1.43	18.4	1.77
	2. Clausocalanus furcatus	1.21	0.99	10.5	1.01
	3. Ctenocalanus vanus	1.10	2.23	9.5	16.20
	4. Haloptilus longicornis	0.88	0.49	7.6	0.70
	5. Mesocalanus tenuicornis	0.72	0.45	6.2	1.54
	6. Nannocalanus minor	0.51	0.48	4.4	1.62
	7. Clausocalanus arcuicornis	0.47	0.42	4.0	0.51
	8. Pleuromamma gracilis	0.47	0.73	4.0	1.95
	9. Clausocalanus parapergens	0.41	0.63	3.5	6.24
	10. Lucicutia gemina	0.41	0.26	3.5	1.17
b)	1. Haloptilus longicornis	1.28	0.67	12.0	0.70
	2. Mesocalanus tenuicornis	1.18	0.78	11.1	1.39
	3. Pleuromamma gracilis S.l	1.14	1.56	10.8	2.78
	4. Nannocalanus minor	0.92	0.99	8.7	1.16
	5. Pleuromamma abdominalis	0.73	0.61	6.9	1.51

The ten principal adult species constituted 72 % by numbers. Among these, most striking distribution patterns were observed in C. vanus. Below the 20°C isotherm at 100 m it was heavily concentrated averaging 6.4 m^{-3} in the very north, thus even outnumbered L. flavicornis, but wholly wanting in the south-east. Conversely, H. longicornis reached its distributional range in the north but increased its abundance with temperature attaining third rank in the south. Remarkably, abundance data of immatures of both species paralleled adult distribution patterns closely. L. flavicornis was by far the most important species, ranking first to third within the four depth layers; it particularly predominated in the 50 to 150 m layer (Table 3). Of the ten most abundant adult species all but M. tenuicornis and H. longicornis gave some indication of diurnal vertical migration. Clausocalanus and Lucicutia were found the dominant genera of the study region forming respectively 24.1 and 22.8 % by numbers, of the total adult population.

Copepod community structure. - The samples contained 101 species of calanoid copepods. Of a total of 18% occurring in at least 90% of the samples, 10% were collected at all stations including Mesocalanus tenuicornis, Nannocalanus minor, Clausocalanus arcuicornis, C. furcatus, C. mastigophorus,

Table 3. *Abundance (No. m^{-3}) of the principal calanoid copepod species (adults) for the four depth zones. Average of 49 hauls, light conditions not considered.*

0 - 50 m		50 - 100 m		100 - 150 m		150 - 200 m	
Clausocalanus furcatus	3.64	Lucicutia flavicornis	3.57	Lucicutia flavicornis	2.11	Lucicutia gemina	0.89
Lucicutia flavicornis	2.39	Mesocalanus tenuicornis	1.43	Ctenocalanus vanus	1.87	Ctenocalanus vanus	0.72
Acartia negligens	1.32	Haloptilus longicornis	1.35	Haloptilus longicornis	1.36	Lucicutia flavicornis	0.63
Nannocalanus minor	0.98	Nannocalanus minor	0.79	Mesocalanus tenuicornis	0.89	Haloptilus longicornis	0.63
Clausocalanus mastigophorus	0.96	Clausocalanus furcatus	0.74	Lucicutia gemina	0.65	Clausocalanus parapergens	0.34

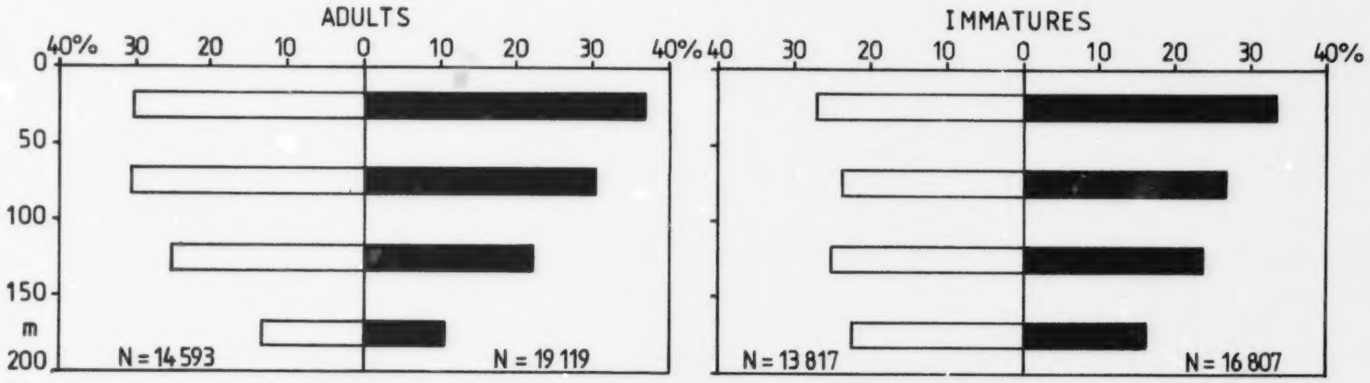

Figure 3. *Vertical distribution of adult and immature calanoid copepods, showing the percentage of total daytime catch (white) and nicht catch (black) per 50-m step.*

Aetideus acutus, Lucicutia flavicornis, Heterorhabdus spinifer, Paracandacia bispinosa, and Acartia negligens. Conversely, 50% of the species numbers had a frequency of less than 20%. Among these, 13% were extremely rare being taken at one station only. Referring to the upper 200 m, species numbers per station averaged 33.2 for adults or 39.8 including immatures. Since nighttime hauls yielded significantly higher species numbers than samples from other periods of the day, artificial night values were achieved comparable to abundance data before. Mean day/night differences regarding species numbers proved nearly identical between northern (10) and southern (9) stations. In Fig. 4 the horizontal distribution of species numbers per station is shown for the upper 200 m. Evidently species numbers were linked, at least partly, with abundance values, particularly, considering the minimum area. Compared to the north, lower species numbers in the south probably resulted firstly from diurnally migrating taxa avoiding higher temperature by submerging to deeper levels (noted in C. vanus), and secondly, from faunal range limitations of temperate to subtropical nonmigratory species. There were more species restricted to the northern subregion than were to southern waters, including twelve and four taxa, respectively, obtained at least once in either area.

Highest numbers of species were reached in the upper 100 m by day, but they were found to rise to the top 50 m during dusk and night (Table 4). Irrespective of light conditions, smallest numbers were generally confined to the deepest level sampled, a fact, ascribed in part to minimum abundance at that depth.

Table 4. *Mean number of calanoid copepod species identified per haul for the four depth zones.*

Depth interval (m)	**Day (n = 27)**		**Twilight (n = 7)**		**Night (n = 17)**	
	No.	**s.d.**	**No.**	**s.d.**	**No.**	**s.d.**
0 - 50	21.6	4.2	25.3	4.7	30.8	6.9
50 - 100	21.6	4.3	21.0	2.7	29.8	6.6
100 - 150	20.2	5.6	21.4	4.2	27.8	7.8
150 - 200	16.6	5.4	17.7	1.6	24.6	5.5

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VERTICAL DISTRIBUTION OF CYCLOPS VICINUS IN LAKE CONSTANCE

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Abstract: In Überlinger See, a bay in the NW of Lake Constance, C. vicinus showed a monacmic seasonal cycle with a maximum in spring, dominated by copepodites I-III. No distinct vertical migration pattern was found. The observed maximal amplitude of migration was 15 m. The resulting alterations in the populations' temperature, food concentration and prey abundance are low. In June the migration of females was most pronounced and may be a predator avoidance mechanism. Food limitation as well as photoperiodicity is dicussed as causal regulation of the monacmic seasonal cycle. The prey consists mainly of copepods (74% - 98%), especially nauplii and CI-III. Only in June did most of the prey organisms consist of Cladocera (66%) especially Daphnia hyalina.

The vertical distribution and migration of C. vicinus was studied during a yearly cycle in Lake Constance. Changes in environmental conditions which could affect the seasonal abundance of C. vicinus, and the impact of its predacious stages on the zooplankton community, are discussed.

METHODS

The study was done in the middle of Überlinger See, a 147 m deep bay in the NW of Lake Constance. From April 1977 to March 1978 the vertical distribution of C. vicinus was studied in monthly 28h-investigations. The animals were sampled with a Schindler-Patalas trap (Volume: 25.8 l, mesh-size: 100 u) at 11 depths (0.5 m - 60 m) every 4h. For the estimation of the vertical phytoplankton stratification water samples were collected at 9 depths (0.5 m - 60 m) every 6h. The amount of phytoplankton (>30 µ) was measured as POC (mgC/l). Zooplankton samples were counted totally. Copepodites I-III, IV-V, males, and females with and without eggs were recorded. The depths of the 20, 50 and 80 percentile of the population were calculated. Using the vertical distribution of C. vicinus and temperature, phytoplankton and possible prey organisms, the mean temperature (t), food-concentration (fc) and prey-abundance (pa) were calculated as weighted means. From these means average values/24h were calculated. The following were considered as possible prey-organisms: cyclopoid and calanoid nauplii and CI-III, Eudiaptomus gracilis (adults and CIV-V), Daphnia galeata, D. hyalina and Bosmina sp. For the cladocerans, the calculations were done separately for adults and juveniles. The calculated prey abundance measures only the predator-prey encounter probability and not the selectivity of the predator.

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RESULTS

1. Abundance

The Überlinger See *C. vicinus* showed a monacmic seasonal cycle. In spring the copepod was the dominant crustacean-zooplankter in the Lake. During summer the CIV exhibited a distinct diapause (Einsle, 1967). From July to October only a few animals were found in the pelagial. From November on, the CIV started to rise from the lake bottom, continuing their development. In May, the population was dominated by CI-III and in the remaining months by older stages. This seasonal abundance cycle is a constant pattern (Einsle, 1975; Schober, 1980).

2. Vertical distribution and migration (Fig. 1).

In April the population was distributed between 10 m and 50 m depth. In May there was an upward shift. Despite the large increase in abundance the population was confined to the uppermost 15 m. This upward shift may be due to the decrease in light penetration caused by the spring algal boom (secchi-depth: April: 7 m, May: 2 m) and was found for all major zooplankton species. No large scale vertical migration was found in either month. In April, however, a migration with an amplitude up to 15 m is possible. In June the population was distributed between 10 m and 50 m (secchi-depth: 13 m). The adult animals did migrate, females migrated more strongly than males. In November the population was again confined to the upper 20 m. In January the population was almost evenly distributed between 10 m and 50 m. No migration was observed in either month. In March the population was distributed in the upper 30 m, and a vertical migration with an amplitude up to 15 m was observed.

3. Temperature

The average minimum temperature/24h for the population of *C. vicinus* was 4.2°C (Jan.), the maximum 10.4°C (Nov.). The maximal change experienced by migrating individuals was 2.8°C in June. In April, January and March there was little or no temperature stratification of the lake (Δt 0 m-60 m $\leq$ 1.0°C). Thus average temperatures/24h reflect the lake temperatures and are independent of vertical distribution and migration. The highest average temperatures/24h were found in May and November, when the population was restricted to the upper water layers. The influence of the increased temperature stratification in June is reduced by the downward shift of the population.

4. Nutrition

4.1. Copepodites I-III (Fig. 2).

The CI-III are regarded as mainly herbivorous or as able at least to cover their metabolic demands by herbivorous feeding (Schober, 1980). The average food concentration/24h available to the CI-III depended on the seasonal phytoplankton biomass. The maximum of 0.751 mgC/l was found in May during the spring algal bloom. In the remaining months, the average food concentrations were below 0.155 mgC/l. Differences due to changes in vertical distribution or migration of CI-III were

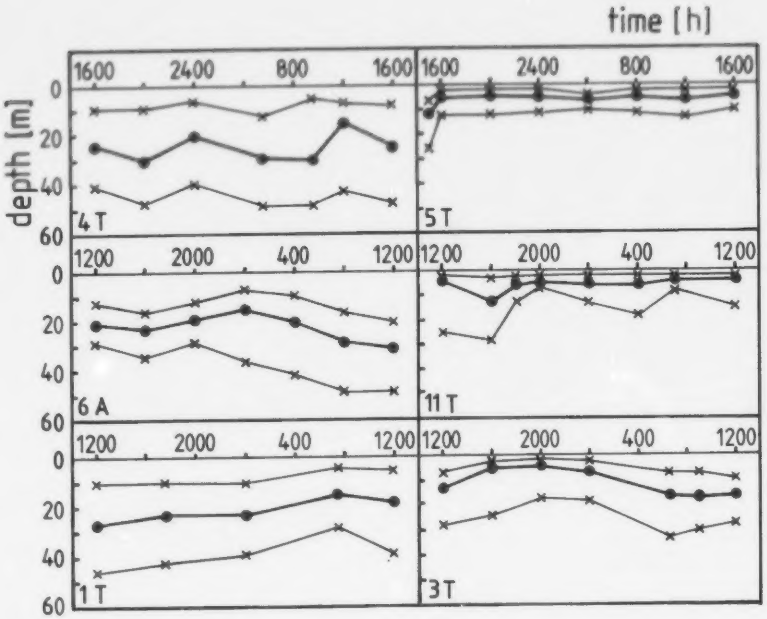

Figure 1. *Vertical distribution and migration of C. vicinus: depth of the 20(x)-, 50(0)- and 80(x)- percentiles of the population, arabic numbers: months, T: total population, A: adult population.*

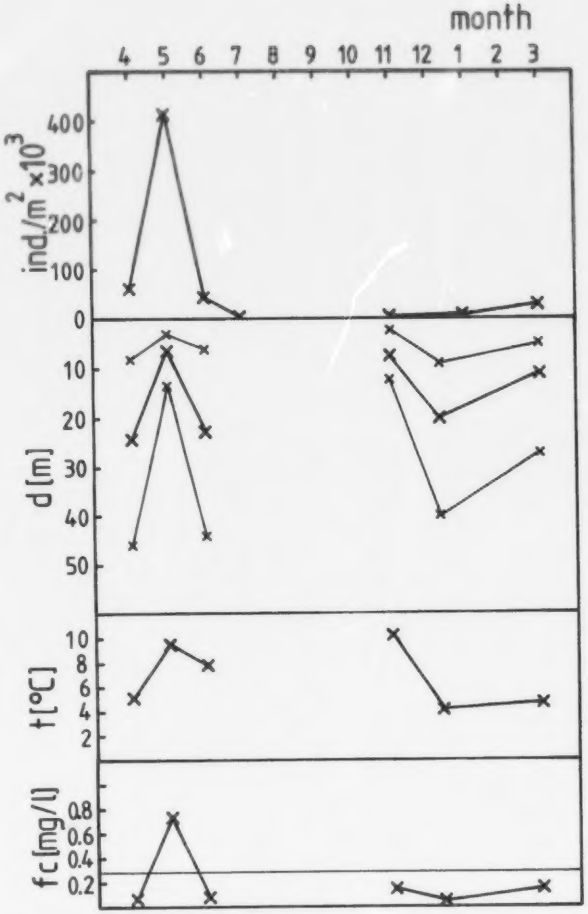

Figure 2. *Average values/24h for copepodites I-III: abundance, depth of 20-, 50- and 80- percentiles, temperature, food concentration.*

≤ 0.029 mgC/l. In laboratory feeding experiments Schober (1980) found a threshold food concentration of 0.34 mgC/l (Scenedesmus, 10°C) and 0.28 mgC/l (Stephanodiscus, 10°C) for the CI-III of the C. vicinus population of Überlinger See. Only during the spring algal bloom in May did the average food concentration/24h exceed these threshold concentrations. Since the POC-estimation includes detritus, the nutritional value of the natural phytoplankton assemblage is probably lower than that of pure Scenedesmus and Stephanodiscus. Whether the average food concentrations/24h exceed the threshold concentrations after applying the neccessary corrections for lower temperatures has to be ascertained by further studies.

4.2. Copepodites IV-V, Adults (Figs. 3, 4).

The CIV-V and the adult animals are carnivorous (Brandl and Fernando, 1975, 1978). Their herbivorous feeding capability is strongly reduced (Schober, 1980). From April to June the average prey abundance/24h increased, from November to March little variation occurred (Fig. 3). The contribution of the major zooplankton species to the average prey abundance/24h (P) is given in percent in fig. 4. Copepods contributed between 74% and 98%, nauplii and CI-III dominating always. Only in June did the proportion of copepods drop to 34%, while that of cladocerans, especially D. hyalina, rose correspondingly. The average prey abundance/24h (P) depends on the abundance, vertical distribution and migration of predator and prey. The average lake abundance/24h (L) of prey organisms depends only on abundance. As both abundances are similar (Fig. 4), the prey abundance was determined mainly by the seasonal abundance of prey organisms. Only the observed differences for D. hyalina in November were clearly caused by the vertical migration of the cladoceran (Stich and Lampert, 1981), and can be interpreted as a predator avoidance mechanism.

DISCUSSION

No distinct vertical migration pattern was found for C. vicinus in Überlinger See. When the animals are concentrated in the upper water layers the low amplitude of vertical migration is difficult to detect (Einsle, 1975). The observed maximal amplitude of migration was 15 m. The resulting alterations in the populations' temperature, food concentration and prey abundance were small. In June, the vertical migration of females was most pronounced. Hairstone et al. (1983) found that females of Diaptomus sanguineus, especially those carrying eggs, were more visible than males and that added visibility accounted for higher predation and mortality. To what extend vertical migration of female C. vicinus acts as a predator avoidance mechanism requires further studies. The changes in vertical distribution coincided with the alterations of light transmission, which is among other factors dependent on the seasonal phytoplankton concentration. Light sensitivity of copepods has been demonstrated by Einsle (1967, 1975).

The downward shifting of the population in June is also influenced by the beginning of diapause of the CIV. Einsle (1975) reported this shifting for the CI-III also. Immigration of C. vicinus into Lake Constance coincided with the beginning of eutrophication (Kiefer, 1963). With the beginning of summer the CIV exhibit a distinct diapause, and the CI-III are inactivated and die off (Einsle, 1975). In Überlinger See this results in a monacmic seasonal abundance cycle. In more eutrophic parts of Lake

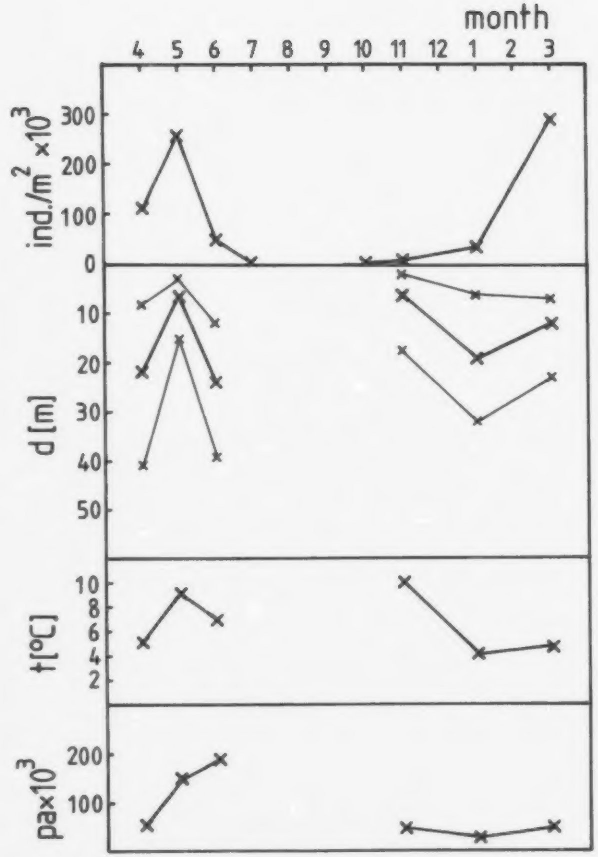

Figure 3. *Average values/24h for copepodites IV-V and adult animals: abundance, depth of 20-, 50- and 80- percentiles, temperature, prey abundance.*

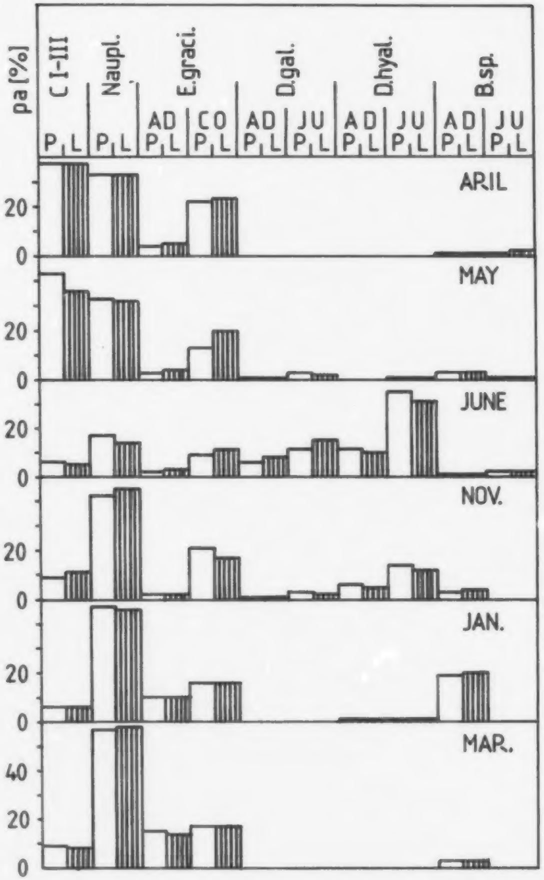

Figure 4. *Average values/24h for prey abundance (P) and lake abundance (L) CI-II, Naupl.: cyclopoid and calanoid copepodites I-III and nauplii, E. graci.: Eudiaptomus gracilis, D. gal.: Daphnia galeata, D. hyal.: Daphnia hyalina, B. sp.: Bosmina spec., Ad: adult animals, CO: copepodites IV-V, JU: juvenile animals.*

Constance and other lakes diacmic or polyacmic cycles are found (Straskraba, and Hrbacek, 1966; Einsle, 1975; Stebler, 1979; George, 1976). If the CI-III are herbivorous, or if their further development depends mainly on herbivorous feeding, the monacmic cycle of the C. vicinus population in Überlinger See might be caused by food limitation. Only in May did the average food concentration/24h of the CI-III exceed the threshold concentration. The spring algal bloom in May is followed by a period of low phytoplankton concentration (Lampert and Schober, 1978). The food-limited CI-III die off, and lacking further recruitment the development cycle is interrupted. In more eutrophic lakes the development of the CI-III can continue, resulting in a bi- or polyacmic cycle.

The coincidence of decreasing C. vicinus numbers and increasing Daphnia numbers has often been reported and interpreted as a result of a causal predator-prey interaction (Straskraba, and Hrbacek, 1966; Brandl, 1973; Lampert, and Schober, 1978; Lampert, 1978). Brandl, and Fernando (1975, 1978) emphasize the size dependent selectivity of carnivorous C. vicinus. In their experiments small species and, within species, small specimens of stages were selected. Selectivity was highest for rotifers, nauplii and calanoid CI-III. Furthermore they found an assimilation efficiency of 50% to 70% for nauplii and less than 35% for cladocerans. Prey selection by carnivorous C. vicinus will be influenced by the relative size of the available prey organisms. If Daphnia represents a "small" organism in the offered prey, a positive selection is found (Schober, 1980), if representing a "large" prey organism negative selection occurs (Brandl and Fernando, 1978). Thus the selectivity of carnivorous C. vicinus depends on the natural abundances and relative sizes of prey organsims. During spring the prey abundance in Überlinger See comprises more than 70% nauplii and CI-III, small prey organisms for which C. vicinus has a high assimilation efficiency. Prey abundances and prey preferences are not coinsistent with the interpretation of decreasing C. vicinus abundance and increasing Daphnia abundance as a result of direct predator-prey interaction. The impact of carnivorous C. vicinus on the zooplankton community requires further study.

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CASES OF HYPER-ASSOCIATION IN COPEPODA

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During the First International Conference on Copepoda, I lectured on siphonostomatoid Copepoda forming galls on stylasterine corals in the South Pacific. At the present occasion, I present some data on Copepoda parasitizing Polychaeta which in their turn form galls on hard corals of the groups of Octocorallia and Stylasterina.

The polychaetes live in almost closed galls or gall-like galleries, as in cages from which they cannot leave. They may be called, at least, "irritating associates", causing reactions of the host's tissues. The Copepoda found on these associates may be termed "hyper-associates", in analogy with the term "hyperparasites".

The table shows the existence of five species of Copepoda associated with gallicole Polynoidae and closely related Aphroditidae, in the southern Indian and Pacific Oceans, all from deeper waters (bathyal zone). Two facts are striking: (1) The gall-inducing Polychaeta belong to, or are closely related to, normally free-living, benthic genera; (2) The copepods as well belong to families and genera known to parasitize free-living polynoid/aphroditid polychaetes.

Table 1.

Host and locality	**Associate no. 1 (gallicole Polychaete)**	**Associate no. 2 ("hyper-associate") (Copepoda)**
Corallium profundum Dana, 1846 (Octocorallia) Comoro Is., 510-475 m	Polynoe caeciliae Fauvel, 1913	Herpyllobiidae gen. ? sp. ?
Errina sp. (Stylasterina) Croizet Is., 365-485 m	Lagissa irritans Marenzeller, 1904	Herpyllobius n. sp Herpyllobius n. sp.
Stylaster sp. (Stylasterina) Réunion Is., 350-750 m	Harmothoe coralophila Day, 1960	Selioides n. sp.
Crypthelia sp. (Stylasterina) New Caledonia, 585-600 m	Polynoidae gen./sp.	Eurysilenium n. sp.

Notwithstanding the taxonomic ordinariness of the associates and their hyper-associates, these cases are not devoid of interest, since they are - as far as I know - the first instances of hyper-association recorded for Copepoda (not counting some borderline cases of Copepoda parasitizing polychaetes that live loosely ectoassociated on the body surface of echinoderms).

EGG DEVELOPMENT TIME AND ACCLIMATION TEMPERATURE IN ACARTIA TONSA (DANA)

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Abstract: Egg development time in Acartia tonsa is shown to correspond with the time required for full temperature acclimation of egg hatching response and is about 24 to 48 hours at 20°C.

The responses of poikilotherms and poikilotherm development rate to temperature and temperature changes are the most investigated physiological responses in marine invertebrates (see Bullock, 1955; Prosser, 1973; Precht et al., 1974). The questions of how organisms respond to environmental changes lead naturally to experiments or observations to answer specific questions. The effect of temperature on survival (Gonzalez, 1974), tolerance (Bradley, 1978), birth and death rates (Keen and Nassar, 1981), egg development rates (Burgis, 1970; Corkett, 1972; Bottrell, 1975) and timing of diapause (Hairston and Munns, 1984) ultimately contribute information for estimates of secondary production and population dynamics (Edmondson et al., 1962). The time periods over which these responses are manifested are also of interest.

Acclimation of temperature occurs in poikilotherms, and often quickly. Halcrow (1963) found Calanus finmarchicus oxygen consumption acclimated within three days after a temperature change. Acclimation to increased temperature occurs quite rapidly (less than 24 hours) in the calanoid copepod Eurytemora affinis (Bradley, 1978), which also acclimates to decreased temperature but less rapidly. Palmer and Coull (1980) suggested that the harpacticoid copepod (Microarthridion littorale) acclimated during the two-day period over which temperatures were adjusted prior to the start of their experiments.

Landry (1975) suggested egg hatching rates for the marine calanoid copepod Acartia clausi were affected by the temperature history of the female parent. He reported the hatching rate of A. clausi eggs spawned by a winter population was significantly faster than the hatching rate of eggs from the summer population when incubation temperatures were above 19°C. Landry also suggested that adaptation of winter acclimated animals to summer conditions is a slow process requiring more than one generation at 20°C.

Although Uye and Fleminger (1976) and Uye (1980) failed to confirm Landry's (1975) results and concluded that eggs produced by A. clausi and A. steueri have similar physiological properties throughout the year, the question of the effect of parental temperature history still remains.

Tester (1982, and in preparation) tested the temperature lability of A. tonsa eggs (subitaneous) before and after they were laid. Results of these experiments indicated parental acclimation temperature and egg incubation temperature had significant effects on the hatching time of A. tonsa eggs. In laboratory experiments egg hatching times fully acclimated to temperature changes within days and hatching times of eggs from field collected A. tonsa demonstrated acclimation of hatching times does occur in the field and responds to time periods of less than one generation.

Since parental acclimation temperature is a factor in the hatching time of A. tonsa eggs it becomes important to know the time required for an oocyte to develop into an egg. Is the yolk labile to temperature and over what time does the yolk accumulate? Marshall and Orr (1972) reported that occasionally stage V Calanus females were found with a large, well-developed ovary and they thought some stage V females could be ripe when they molted to stage VI.

The purpose of this research is to determine the period required for A. tonsa eggs to develop in the ovary, and therefore, the time they can be influenced by the temperature of the female parent.

MATERIALS AND METHODS

Algae were labeled with ^{14}C and fed to immature copepods (stage CI) throughout their development to adults (stage CVI). In a second experiment labeled algae were fed to adults. If eggs accumulate yolk over a long period, the eggs of the copepods fed labeled algae during their development from CI to CVI would be expected to show a higher level of activity than the eggs of adults fed labeled algae after maturity.

The methods used for the ^{14}C experiments were modified from Copping and Lorenzen (1980). Two-liter cultures of unicellular Thalassiosira weissflogii (5×10^3 cells ml^{-1}) were adjusted to pH 3 with NaOH, innoculated with 40 uci of $NaH^{14}CO_3$ (Amersham[1], specific activity 652 μci mg^{-1}) and cultured under constant illumination at 20°C. After approximately four days the uniformly labeled algal cultures, ready to serve as food, were centrifuged at 5,000 rpm in a Sorvall centrifuge for three minutes to concentrate the algae. The supernatant was decanted and the algae resuspended in sea water of 15 °/oo salinity before being used as food for the copepods.

Eggs were sampled either after the copepodites reached maturity or from 3.5-96 hours after the adult A. tonsa were given labeled algae as food. Unlabeled algae were then substituted for labeled algae and eggs were again taken 24-48 hours later. All egg laying periods were two hours and all samples were done in triplicate. Eggs from these experiments were screened from the cultures, kept at a constant temperature of 20°C, suspended in seawater (12°/oo salinity) and transferred through three rinses to avoid contamination by fecal pellets. Samples of the eggs were then filtered onto one cm Millipore filters (5 µm pore size) and washed twice with 0.5 N HCl to remove ^{14}C remaining on the filter as inorganic carbonate. The filter was then quickly rinsed with distilled water to remove the acid and placed on blotter paper, and the eggs were enumerated. Both the filter and eggs were placed in a glass scintillation vial with 25 ml of organic counting scintillant (OCS 196322 Amersham). After 48 hours, the samples were counted in a Beckman liquid scintillation counter for their entire ^{14}C pulse height spectrum at 2% error. As a control, two hour old unlabeled eggs were allowed to incubate for one hour in medium from the ^{14}C copepod culture to determine if newly laid eggs would take up ^{14}C directly from the medium. These eggs were then treated as were the experimental eggs. This ^{14}C blank and a standard blank of unlabeled eggs were run in triplicate.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

The uptake ^{14}C labeled food was rapid (Fig. 1); egg samples taken 3.5 hours after the feeding of labeled algae showed activity above the baseline. After 24 hours the activity level of the eggs was relatively constant in both the eggs produced by adults fed labeled algae and the first eggs laid by the copepods fed labeled algae since the CI stage. The loss of activity of the eggs was also rapid; within 48 hours after females had been given only unlabeled food, the activity level had dropped from an average of 410 cpm egg^{-1} to less than 100 cpm egg^{-1}.

From Tester (1982) when temperature of stock cultures of *A. tonsa* was raised 5°C from 20°C to 25°C for as little 24 hours, the time to 50% hatch of eggs from this culture was 13.2 ± 3.7 hours which was within the 95% confidence interval of the control for this experiment (Fig. 2). When the reciprocal experiment was done, stock cultures maintained for 1 generation at 20°C were kept for 46 hours at 15°C, after which, time to 50% hatch of the eggs was 45.0 ± 3.9 hours (control = 40.1 ± 3.9 hours).

The time required to acclimate egg hatching time to a 5°C temperature change, either higher or lower is consistent with the time required for *A. tonsa* eggs to develop under the influence of the changed temperature.

DISCUSSION

Hilton (1931) recorded the most rapid period of yolk formation in *Calanus finmarchicus* was at the stage of half-grown oocytes. Eggs from the females fed labeled algae from CI through CVI stages and eggs from females fed labeled algae for only 24 hours at 20°C were uniformly labeled. Either *A. tonsa* eggs are produced rapidly at 20°C, or the exchange between the carbon pool in the rest of the body and the ovary is rapid, or both. Copping and Lorenzen (1980) found the specific activity of *C. pacificus* equaled that of the ^{14}C labeled phytoplankton 48 hours after first exposure to it. Estimates of daily egg production of *A. tonsa* evidence that eggs are produced quickly and nearly continuously. Tester and Costlow (1981) reported 28 eggs $female^{-1}$ d^{-1} at 20°C, Parrish and Wilson (1978) found 25.8 eggs $female^{-1}$ d^{-1} at 18°C and egg production was only 50% after one day of starvation. When feeding resumed after 3 days the egg production assumed pre-starvation levels by the third or fourth day. In a similar study using *A. clausi*, Uye (1980) found egg laying to respond in the same manner as in *A. tonsa* with respect to food availability.

To fully appreciate the complexities and the magnitude of thermal effects of the physiology and acclimation responses of egg hatching times, details of the thermal history of the parents and egg incubation temperature are required. Bullock (1955) warned that it is mandatory to measure rate-temperature curves of poikilotherms using animals that have been completely acclimated to the temperature at which the rate of the response is being measured. Edmondson (1960), working on the hatching of rotifer eggs, found a marked difference between the temperature duration curves for acclimated and non-acclimated animals. Bell (1983) reiterates the need to build tactical models of life histories in which predictions are based on the detailed study of particular cases. Predictions of *A. tonsa* egg hatching rates or population parameters based on birth rates should be calculated carefully from empirically derived data for the local population in question.

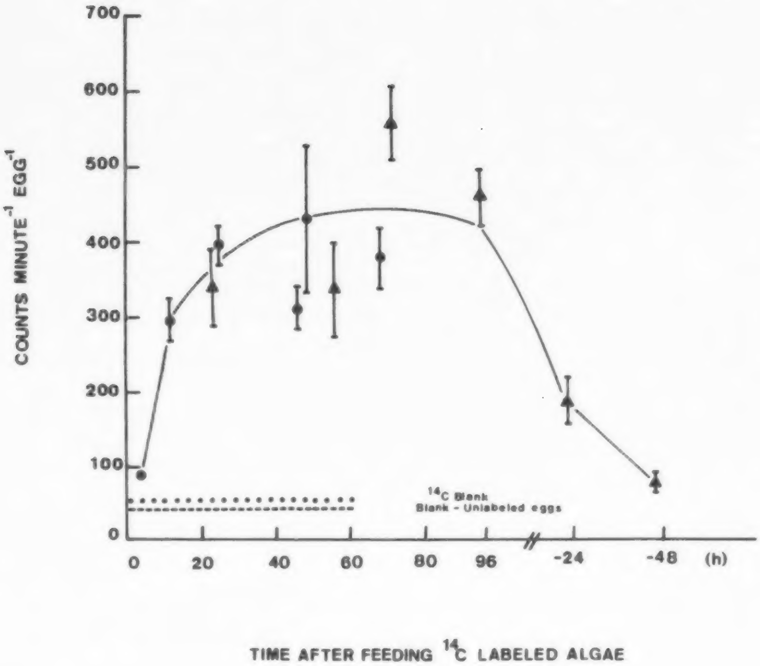

Figure 1. *Activity of eggs from* *Acartia tonsa* *after being fed* ^{14}C *labeled algae. Adults were exposed to the labeled algae for 96h after which unlabeled algae was substituted for the labeled algae and the activity of the eggs was monitored for another 48 h. Standard deviations are shown. Triangles represent data from* *A. tonsa* *on labeled algae since stage CI. Closed circles represent data from adults fed labeled algae.*

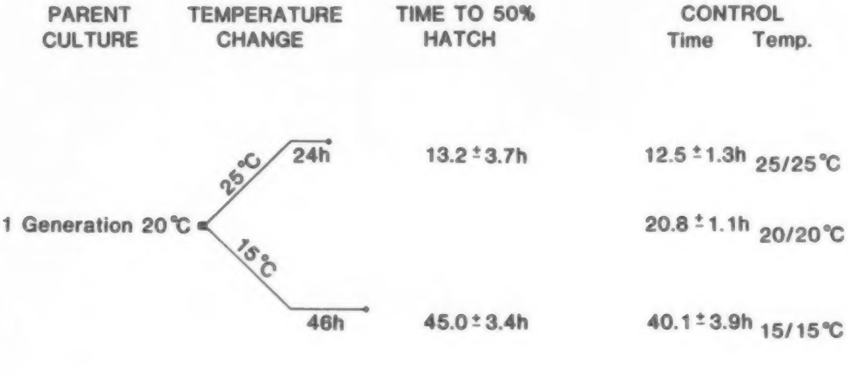
PARENT CULTURE
TEMPERATURE CHANGE
TIME TO 50% HATCH
CONTROL
Time
Temp.
1 Generation 20°C
25°C
24h
15°C
46h
13.2 ± 3.7h
45.0 ± 3.4h
12.5 ± 1.3h
25/25°C
20.8 ± 1.1h
20/20°C
40.1 ± 3.9h
15/15°C

Figure 2. *Time required for egg hatching rate of* *Acartia tonsa* *from parental cultures which experienced a temperature change to equal the hatching rates of fully acclimated cultures (controls). Contral temperatures are long-term acclimation temperature of parent culture and egg incubation temperature.*

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BENTHIC DISTRIBUTIONS OF PLANKTONIC COPEPODS, ESPECIALLY *MESOCYCLOPS EDAX*

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Abstract: *Mesocyclops edax* periodically had a strongly benthic distribution in three lakes examined with both benthic and planktonic sampling devices. In Wintergreen Lake, Michigan, adult *Mesocyclops* were more abundant in sediment traps deployed in the anaerobic hypolimnion than in vertical net hauls. In Lake Normandy, Tennessee, diel vertical series of Schindler traps made at a shallow station and at a deep station suggested that *Mesocyclops* was confined to the plankton by a thick ($>$ 6 m) anaerobic hypolimnion, but preferred the benthos when accessible. In Lake Texoma, Oklahoma-Texas, Ekman dredges and diel vertical series of Schindler traps showed that *Mesocyclops* were predominantely planktonic when the hypolimnion was anaerobic. Other cyclopoid and calanoid copepods in Lake Texoma showed less preference for the benthos, or resorted to diapause when a deeper distribution was precluded by an anaerobic hypolimnion.

INTRODUCTION

Many zooplankton species inhabit the benthic environment for a portion of their lives or during certain environmental conditions; such major habitat shifts are usually related to survival strategies. Most studies of benthic distributions of planktonic copepods focus on diapausing stages (eggs or copepodids). Less attention has been given to active stages which only temporarily inhabit the benthos, or to the implications of such behaviors for population studies. This paper presents data from three lakes where we attempted to evaluate the portion of the non-diapausing population which inhabited the benthos. We discuss the implications of these benthic distributions for assessments of population dynamics or life history strategies.

METHODS AND MATERIALS

Samples were collected of planktonic and benthic copepods in three lakes, as described below. All samples were preserved in 4% sucrose formaldehyde and examined with a dissecting microscope at 25-100x. Species identifications were made using Edmondson (1959). In Wintergreen Lake, Michigan, a small hypereutrophic kettle lake (15 ha, $\bar{z} = 3.5$ m, $z_{max} = 6.3$ m), a central station was sampled on three dates in July 1976 in the early afternoon and at midnight. Duplicate vertical net tows of a 30 cm diameter, 137 µm mesh net were taken from just above the bottom (2 m into the anaerobic hypolimnion) to the surface. In addition, paired sediment traps (6.25 cm diameter, 12.5 cm deep) were deployed at 4.5 m in the anaerobic hypolimnion at approximately 1500 hours and collected the following day at approximately 1300 hours. These collections were a part of a study of *Daphnia* population dynamics (Threlkeld, 1979).

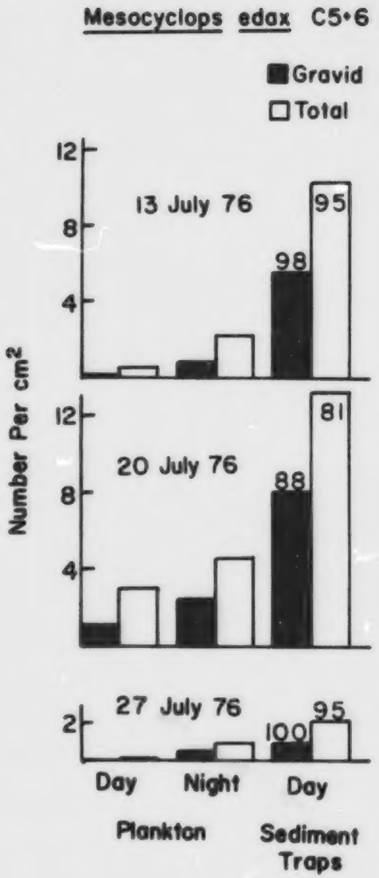

Figure 1. *Densities of Mesocyclops edax stage 5 and 6 copepodids in day and night plankton tows and in sediment traps collected during the day in Wintergreen Lake, 1976. Gravid female and total densities in each type of collection are indicated by solid and open bars, respectively. The percentage of Mesocyclops in the sediment traps as estimated from combined daytime water column and sediment trap totals are presented over the sediment trap portion of the figure (right).*

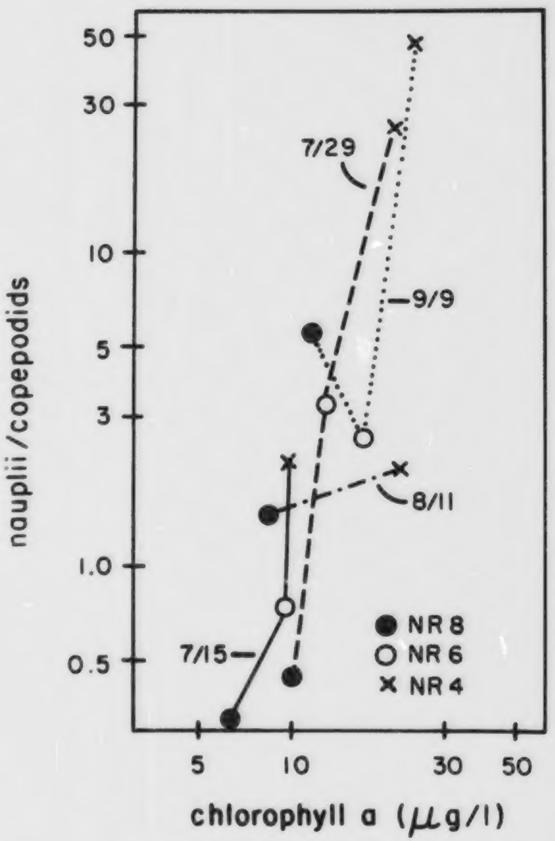

Figure 2. *The ratio of Mesocyclops nauplii to copepodids in Normandy Reservoir at three stations (see Threlkeld, 1983) on four dates in 1980 as a function of algal chlorophyll a.*

In Normandy reservoir on the Duck River, southcentral Tennessee, collections were made at a shallow (z = 8 m) station near the inflow, at a midlake station (z = 10 m) and at a deep station (z = 18 m) near the dam (stations 4, 6 and 8 in Threlkeld, 1983). Duplicate vertical net tows of a 75 cm diameter net with 80 µm mesh were made at noon and midnight on four dates in summer 1980. Duplicate 30 liter Schindler trap samples were taken on three dates at noon and midnight at 2 m depth intervals from the surface to just above the bottom at stations 4 and 8.

In Lake Texoma, an impoundment of the Red and Washita Rivers in Oklahoma-Texas, the vertical distribution and abundance of copepods was assessed on 23 dates in 1982. Samples were collected in the Red River arm of the reservoir at a mid-channel station near the University of Oklahoma Biological Station (Dirnberger and Threlkeld,in press)during daylight and nighttime hours. Duplicate samples were collected with a 30 liter Schindler trap at 2 m depth intervals from the surface to just above the bottom. Duplicate Ekman dredge samples (225 cm^2) were also collected during the day and at night on each sampling date. The duplicate Ekamn samples were subsampled, and washed free of clay through an 80 µm mesh net.

RESULTS

In Wintergreen Lake, Michigan, gravid Mesocyclops edax were virtually absent from the water column during the day, but where abundant in sediment traps retrieved from the hypolimnion. Fig. 1 shows that 88-100% of the gravid Mesocyclops edax in the entire water column were in the sediments during the day. A slightly smaller percentage (81-95%) of total Mesocyclops copepodids were present in the sediment traps during the day. Vertical net tows showed that Mesocyclops was more abundant in the water column at night than during the day. Because sediment traps were not retrieved at night, it is impossible to assess if the differences between densities in day and night vertical net collections reflect light-dependent variation in escape from the net or real diel differences in distribution of Mesocyclops between the plankton and sediment.

In Normandy reservoir, the ratio of Mesocyclops edax nauplii to copepodids was directly related to chlorophyll at the three mainstem stations in Normandy reservoir (Fig. 2). However, the frequency of gravid Mesocyclops in the daytime collections was not related to chlorophyll but was directly related to chlorophyll in the nighttime collections (Fig. 3). The plankton trap samples showed that gravid females remained on or near the bottom at the shallow station during the day, and only moved into the water column at night. At the deeper station (8 in Fig. 1 in Threlkeld, 1983) no change in frequency of gravid females was observed between day and night collections. Because of greater water depth at this station and a more extensive anaerobic hypolimnion (up to 10 m on 11 Aug and 9 Sep 1980), Mesocyclops may have been unable to reach or remain in the benthic habitat during the daylight hours.

In Lake Texoma, Oklahoma-Texas, we documented the incidence of diapause and occurrence of active copepods in the benthos for one year in relation to stratification and a major flood. Lake Texoma was well mixed during th entire year in the area where samples were taken, except for a brief period in late June-late August when anaerobic conditions developed in the lower 2-3 m of the water column. A major flood occurred in mid May which reduced water retention time to less than 5 days in the area that was sampled (Dirnberger and Threlkeld, 1984). Four copepod species were abundant in the samples: Diaptomus siciloides, Eurytemora affinis, Cyclops bicuspidatus thomasi and Mesocyclops edax. Although nauplii (not differentiated according to species), and Eurytemora and Diaptomus copepodids

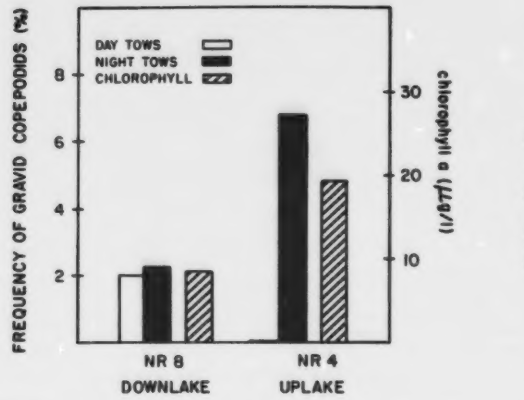

Figure 3. *The frequency of gravid Mesocyclops copepodids at uplake and downlake stations in Normandy Reservoir as determined from day and night vertical net tows in relation to extracted chlorophyll a. Bars represent means for four dates in summer 1980; see Fig. 2 for details.*

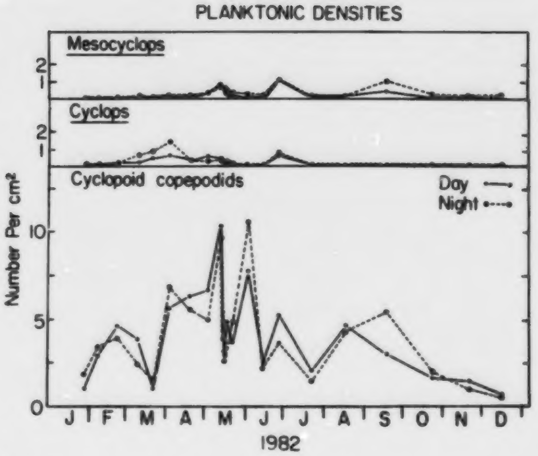

Figure 4. *Densities of Mesocyclops edax and Cyclops bicuspidatus thomasi adults - and copepodids (combined), expressed on an areal basis (individuals per cm^2) for a fifteen meter deep water column in Lake Texoma, 1982.*

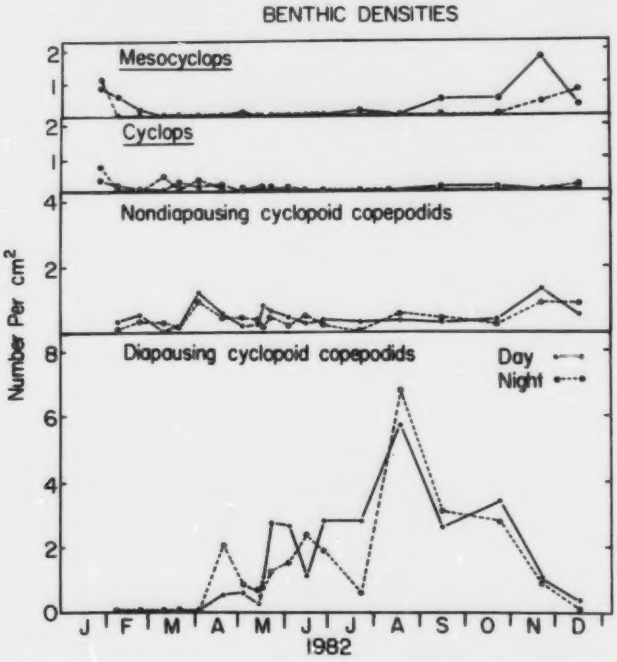

Figure 5. *Densities of Mesocyclops edax and Cyclops bicuspidatus thomasi adults, nondiapausing cyclopoid copepodids and diapausing cyclopoid copepodids, expressed on an areal basis, collected with an Ekman dredge.*

and adults were seasonally abundant in the water column, few were found in the Ekman grab samples. No seasonal variability in benthic occurrence of these taxa was detected. However, Cyclops and Mesocyclops copepodids were seasonally abundant in the sediments following the spring peak of abundance of cyclopoid copepodids in the plankton (Fig. 4 and 5). Although the seasonal increase in diapausing copepodids coincided with the occurrence of a spring flood in Lake Texoma [reminiscent of the findings of Moghraby (1977)], recolonization did not follow subsidence of flood waters. The abundance of nondiapausing cyclopoid copepodids in the sediments did not vary seasonally (Fig. 5). However, active (non-diapausing) Mesocyclops edax were more abundant in the sediment in the fall and winter, and also in day collections rather than at night. There was no diel difference in benthic densities of non-diapausing cyclopoid copepodids and of Cyclops, suggesting that the diel differences in Mesocyclops benthic distributions were real rather than artifacts of collection efficiency (see discussion of Wintergreen Lake results). Comparison of planktonic and benthic contributions to water column densities (Fig. 4 and 5) shows that benthic cyclopoid densities are often equal to or exceed planktonic densities when expressed on an areal basis.

DISCUSSION

Major diel differences occurred in the distribution of Mesocyclops edax in the plankton and benthic samples in the three lakes examined. Mesocyclops edax showed a strongly benthic distribution in shallow oxygenated water columns. Although diapause by late stage copepodids has been noted before (e.g. Vijverberg, 1977; Nilssen, 1978), the tendency (see also Woodmansee and Grantham, 1961; and Coetzee, 1980) of adult Mesocyclops edax to inhabit the benthos during daytime hours suggests three implications not explored before.

1. In Wintergreen Lake and at the shallow station in Lake Normandy, over 88% of gravid Mesocyclops were found in the anaerobic benthos during the day, and were missed by plankton sampling efforts during the daylight hours. This could introduce a severe bias to analyses of population dynamics of the kind noted previously by Gophen (1978) if Mesocyclops shows a diel rhythm in egg laying or if gravid females are underestimated. For example, Nie et al. (1980) noted higher densities of Mesocyclops in near bottom samples; in Tjeukemeer Vijverberg and Richter (1982) suggested that this micro-distributional feature of the population was important to estimates of naupliar recruitment.

2. Much attention has been given to the consequences of fish predation or pond drying on diapause strategies of copepods (e.g. Nilssen, 1978; Hairston et al, 1983; Hairston and Munns, 1984; Hairston and Olds, 1984). Little attention (e.g. Woodmansee and Grantham, 1961, and Chaston, 1969) has been given to the physiological capabilities of copepodids to remain active under anaerobic conditions were they might also be safe from predators. Copepodits in this situation would be better able to take advantage of suitable food supplies and continue to contribute to population growth on a diel basis instead of sacrificing active growth and reproduction for diapause. The relative advantages of diapause and diel migration to the benthos as adaptive strategies (and which occurred in the same lake in this study) need to be explored further.

3. The importance of a diel cycle in diet and predatory impact of Mesocyclops linked to alternation between planktonic and benthic habitats also needs to be explored (Papinska, pers. comm.), as has been done previously with other organisms (e.g. Chaoborus and Mysis) more widely accepted as being meroplanktonic.

ACKNOWLEDGEMENTS

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THE FUNCTIONAL MORPHOLOGY AND HISTOLOGY OF THE GENUS PORCELLIDIUM (COPEPODA, HARPACTICOIDA)

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Abstract: Several species of Porcellidium, especially P. fimbriatum Claus, 1863, have been examined by means of different methods. Both, the external morphology and the histology have been analysed by light microscopy, scanning electron microscopy, and by preparing sections. More detailed studies have been carried out regarding

the mechanical construction of the trunk, especially of the tergites and of the epimeres,
the structure of the mouthparts and of the first leg,
the arrangement of the abdomen with the furcal branches, the fifth leg, and the eggsac,
the most important muscles and their function,
and complementary the position of the great systems of organs:
nervous system, reproductive system, and digestive tract.
All these investigations enable the conclusion how Porcellidium can attach itself to the substrate.

At the previous Congress on Copepoda in Amsterdam there was agreement about the basic body plan of copepods (Tiemann, 1984). Porcellidium differs greatly from this basic plan (Fig. 1). The differences being: the mainly cylindrical body shape is half ellipsoid and shortened by fusion of the P1-segments with the cephalothorax, by fusion of all abdominal segments, and by shortening of the P4- and P5-segments. The antennula is shortened as well, retaining only a few segments, the mandibular palp is larger, the P1 visibly wider and the exopodite of P5 very flat.

Porcellidium consequently is a very specialized harpacticoid genus the nearest less specialized relatives of which are among the tisbids (Lang, 1948, Tiemann, 1975). Porcellidium has not often been examined. Fundamental studies have been made by Claus (1889) and Bocquet (1948), who was the first to assume that Porcellidium has a sucker. In this study the mechanical functions of the genus are to be related with its way of life.

P. fimbriatum (Claus, 1863) from Banyuls, Southern France, has been examined in this study. Whole animals and parts of them have been embedded in balsam. To stain mucus in glands and in the sucker area astra blue in a solution of mild acidity has been used. The surface has been examined by SEM after critical point drying and, particularly, after cleaning with 5% KOH.

Most species of Porcellidium live in the wave zone of the marine littoral and are able to withstand pressure and currents and probably also predators. With the help of a sucker they attach themselves particularly to massive algae.

Their body shape is like a tunnel arch (Fig. 2). The cuticle is relatively thick and sclerotized, the rostrum projects and the short first antennae are at its sides. The ventral side of the rostrum and cephalothorax is widened and thickened and forms a firm support against the substratum. In the cephalothorax there are apodemes resembling columns. The following tergites (2 in the female, 3 in the male) form round arches which are interconnected by paired joints and are also connected with the cephalothorax (Fig. 11). The P5-segment and the almost completely fused abdomen form the back end

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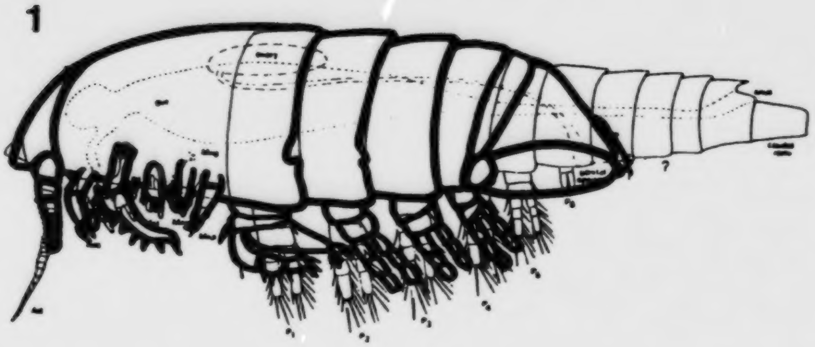

Figure 1. *Schematic representation of the body-form of Porcellidium, compared to that of the ancestral copepod (thin lines, after Boxshall, Ferrari and Tiemann).*

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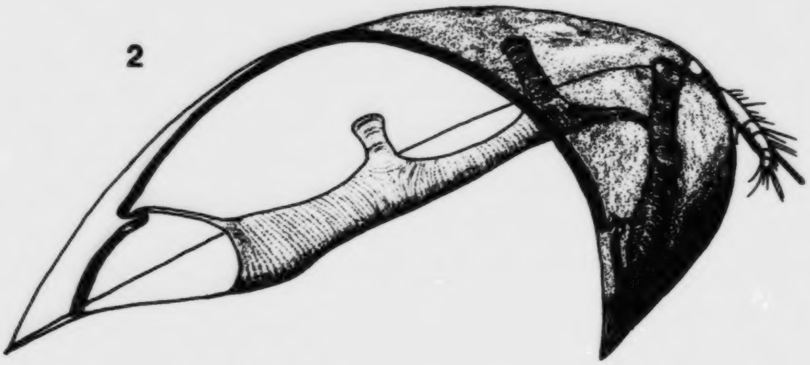

Figure 2. *Porcellidium fimbriatum* ♀, *cepalothorax, inner view.*

of the arch. Both furcal branches and both P5-exopodites close the arch at the back. In the female the large abdomen, the lengthened furcal branches and the very large P5 make room for the egg sac. These three structures are smaller in the male. In addition, along the entire edge of the body there is a hyaline membrane which improves contact with the substratum. Of all the appendages only the first antennae project from underneath the arch. It is with them and the eyes that the animal senses its surrroundings. The second antennae, mouth parts and swimming legs as well as the egg sac are protected under the strong, arched tergite plates.

The gnathobase of the mandible is strongly built having a structure similar to that of the other harpacticoids, while the mandibular palp is extremely enlarged, partly flat. Its entire outer edge is covered by thick and soft, narrowly fimbriated setae (Figs. 5, 7).

The delicate first and the stronger second maxilla remain unchanged. The maxilliped is broadened, distinctly pilose on the posterior margin and has two weak claws apically.

P1 is strikingly broad. A narrow base which has a thick seta on its outer edge lies on the large intercoxal plate. The endopodite has two segments, is of a wide trapezoidal shape and carries 2 so-called claws. Judging from their fine structure these setae are more likely to be rakes (Fig. 8), because they are covered with a row of thin-walled membranes. The exopodite has soft, thickened and narrowly fimbriated setae. From the ventral view of the "mouth-part"-area it is thus clear that the different parts form a composite structure integrating all of these apppendages: there is a ring of the soft, narrowly fimbriated setae arising from the median labrum, the mandibular palp, the outer edge of the base of P1, the P1-exopodite and the P1-endopodite claws. This system is complemented by additional rows of setae on the P1-endopodites, on the back edge of the maxillipeds and on the labrum. In SEM it even appears that the outer ring is enclosed by a glassy mass which envelopes and pastes all plumose setae (Fig. 3, 5, 6). A histochemical analysis showed that this mass can be coloured by phtalocyanine dyes which is characteristic for acid mucopolysaccharide (Fig. 4). When five specimens were stained with astra blue two blue spots appeared in the epimeres of the cephalothorax; they probably represent the mucus glands. Their duct to the surface has as yet not been identified.

All this goes to show that Porcellidium possesses a large ventral sucker which is composed of elements of different appendages and is sealed by a complete ring of mucus covered fimbriated setae (Fig. 3). The following experiments were carried out to further test this assumption. Fixed specimens of P. fimbriatum are bent somewhat ventrally and easily attach and stick to an even surface. Thus the sucker remains functional even in dead specimens. After a few seconds however, the sucker yields and with a little jerk the specimen becomes detached and resumes its usual form. To test the functional capability of the sucker, different parts were removed from the ring, for example the front part of the mandibular palp. The result is that whenever a ring is no longer complete, firm suction becomes impossible. This shows that the ring functions as a seal. Apart from a sealing edge, suckers need a mechanical system to produce a low pressure inside. In animals this can be achieved by the action of ring muscles, elastic structures or muscles which lift the centre of the sucker (Nachtigall, 1974, Schliemann, 1970). The latter mechanism is effective in Porcellidium as has been demonstrated by histological studies.

There are strong dorsoventral muscles (Fig. 9) which stretch from the dorsal wall of the cephalothorax to a tendon attached to a sternal skeletal structure, here called hypostomal clasp. When these muscles contract, the ventral body surface with the posterior mouth parts is raised a little and a low pressure is produced which causes the sucker to adhere.

The following measurements and calculations have been made in order to test whether there is any

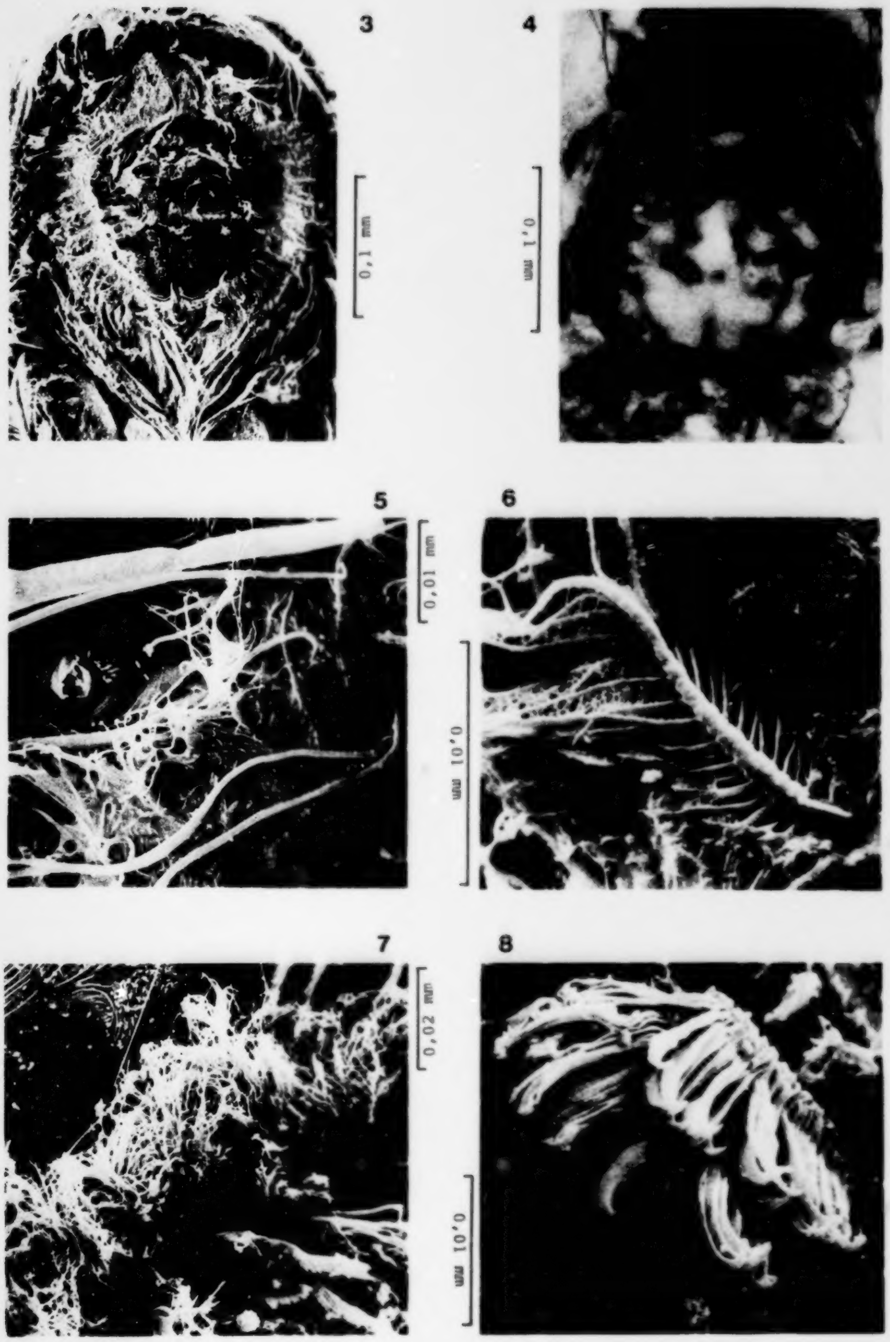
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Figure 3 - 8. *Porcellidium fimbriatum* ♀, *the sucker and its details. Fig.* 3. *Ventral view, SEM; Fig.* 4. *Mucus ring, stained with astra blue, LM; Fig.* 5. *Mandibular palpus, mucus setae, SEM; Fig.* 6. *P1, mucus seta, SEM; Fig.* 7. *Mandibular palpus, plumose setae, cleaned with KOH, SEM; Fig* 8. *P1 endopode, "claws", cleaned with KOH, SEM.*

relation between the size of the sucker and that of the muscles:

1. The inside of the sucker which can be lifted is approximately 10^{-2}mm². If the inside is enlargened by 20%, the result is a force of 2×10^{-4}N to the substratum.
2. The dorsoventral muscles attached to the hypostomal clasp are approximately 10^{-4}mm² in cross-section, all four together 4×10^{-4}mm². The absolute muscular force of a striated crab muscle is approximately 50 N/cm² (Laskowski and Pohlit, 1974, Buddenbrock, 1961). For Porcellidium the sucker muscular force would be approximately 2×10^{-4}N.

This shows that there is a definite relationship between the size of the sucker and that of the muscles. As the absolute mass of Porcellidium is only 10^{-5}g, the animal can attach itself very effectively.

It has also been discussed, (Noodt, 1957) that adhesion may be reponsible for the attachment of Porcellidium to the substratum. According to Bergmann and Schäfer (1965) the adhesive force for solid bodies moistened by water is 5×10^{-3}N/cm². Applied to Porcellidium the result is 5×10^{-7}N adhesive force when the entire sucker size is approximately 1×10^{-2}mm². This force is approximately 3 decimal indices below that of the sucker and shows that adhesion does not play an important role. A gluey secretion may indeed contribute to a more effective adhesion; yet, evidence and more precise tests for Porcellidium are lacking.

In contrast to what has been said about the appendages that are part of the sucker, the swimming legs P2, P3, and P4 are hardly transformed. They allow the animal to swim when leaving the substrate.

Porcellidium is not capable of winding movements because there are tergite joints on both sides of the segments, but dorsoventral bending movements are possible allowing the body to adapt to the substratum. For ventral flexure ventral longitudinal muscles are used which stretch between the cephalothorax and the sternite of the P5. In contrast to the basic plan of harpacticoids the ventral longitudinal musculature is very reduced. The dorsal longitudinal musculature for counter-movements consists of a bundle of parallel, narrow muscles attached to the sides of cephalothorax and stretching into the P2 and P3 segments. They are followed by muscles beginning at the front edge of the abdomen. The musculature for movements of the pars molaris of the mandible can serve as an example for the interplay of a muscle group; the main chewing musculature inserts at the connective tissue tentorium in the center of the body while the extensores are attached to the cephalothorax.

The digestive tract shows the same structure as that of related harpacticoid taxa (Fig. 10). Starting with an esophagus which is equipped with a complicated system of constrictor (narrowing) muscles and with dilatators stretching to the body wall or tentorium it continues as a voluminous midgut which has a small blind sac at the front and merges over a narrowing sphincter into the hindgut leading through the split-shaped anus dorsal of the furca to the outside.

The central nervous system is so entirely fused that the distinct ganglia cannot be recognized. Brain and subesophageal ganglion are joined by wide connectives. As a massive paired cord at the end, the subesophageal ganglion and the close-by thoracic and abdominal ganglia extend as far as into the P3-segment.

The reproductive system has some particular features due to the lack of sufficient place in the abdomen. The paired oviduct emerging from the unpaired ovary separates into branches in the cephalothorax and peraeon. In the male the mature spermatophore extends from the P2-segment to the abdomen.

On the whole Porcellidium is a typical inhabitant of the phytal in strongly agitated coastal waters.

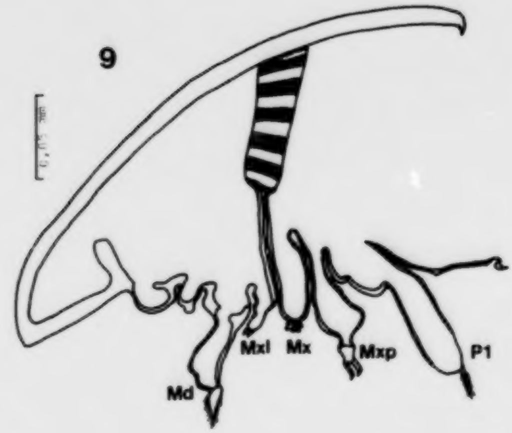

Figure 9. *Porcellidium fimbriatium* ♀, *cephalothorax, longitudinal paramedian section, with the sucker-muscle and sucker-tendon.*

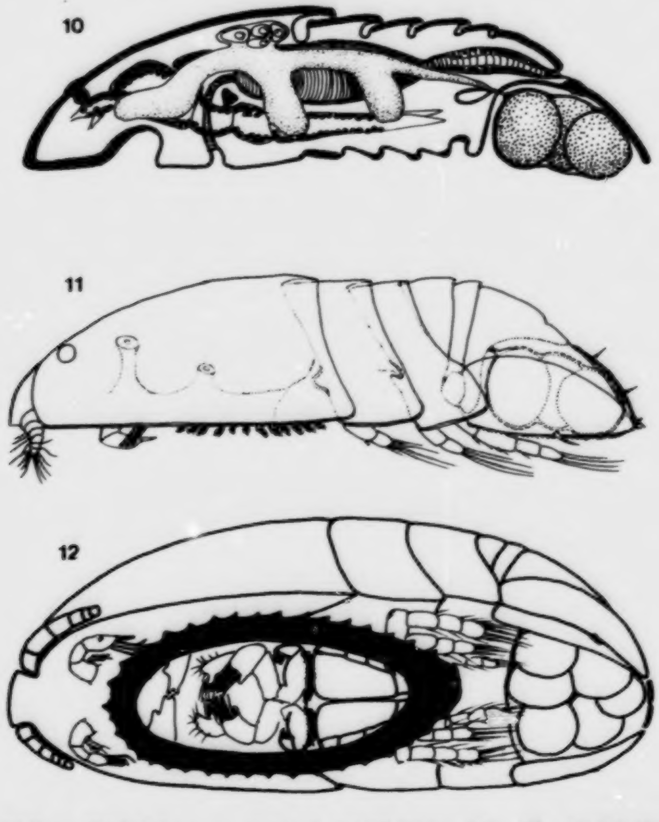

Figure 10 - 12. *Porcellidium fimbriatum* ♀, *general morphology. Fig. **10**. longitudinal section, central nervous system (heavily dotted), digestive tract (striated) and reproductive system (lightly dotted); Fig. **11**. lateral view, with apodemes and tergit joints; Fig. **12**. Oblique view from below with the mucus sucker (drawn dark).*

With its sucker it can attach itself tightly, and in the interval between two waves it can swim about smoothly close over the substratum (Fig. 12). When sucked fast it can scratch its food (green algae, diatoms, detritus) from the substratum. This is done with the mouth parts which are inside the sucker. Even during praecopula when both animals lie behind one another, they can adhere to the substratum with the sucker. When later the female's egg sac is formed, it lies under the body protected from water action.

Many copepods, especially the parasitic Caligoidea, have suckers; also in the Harpacticoida there are other examples as the nauplius of Scutellidium and the adult of Discoharpacticus (Noodt, 1954). These suckers are analogous structures. Only in Porcellidium are they formed by two widely separated appendages, mandible and first leg as well as the labrum. In contrast, the suckers of the adult Scutellidium and Saccodiscus are probably homologous. They are however, morphologically not as perfect as the sucker of Porcellidium.

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ON ARTICULATIONS IN THE FURCAL SETAE OF CALANOID COPEPODS AND THEIR ROLE IN SWIMMING MOVEMENTS

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Summary: From material of Chirundina streetsii it has been established that breaking planes and articulation sites may not only occur in the two intermediate terminal setae of the furca, but also in the lateral and medial ones, or vice versa. Both types of modified sites are described from all four large furcal setae, and their possible functions are discussed. A comparison with the furca of Euchirella messinensis is made.

INTRODUCTION

In a previous paper (Von Vaupel Klein, 1982b), I have described articulations ('modified sites') present in the natatory setae on the swimming legs of female Euchirella messinensis (Claus, 1863) (family Aetideidae). The possibility that such joints, combined with muscular action, might be functional in providing the necessary rigidity-flexibility variation in, respectively, the powerstroke and the recovery stroke of a swimming action, has been discussed as well. As regards the large caudal setae of the furca, I have invariably referred to modified sites found in these as 'breaking planes' only (cf. Von Vaupel Klein, 1980, 1982b). From the study of another aetideid, Chirundina streetsii Giesbrecht, 1895, it became evident, however, that in fact the situation in the furcal setae is more complicated. The actual conditions as presently interpreted, will be outlined in the present contribution.

MATERIAL AND METHODS

Preparative procedures and observation techniques were the same as stated earlier in Von Vaupel Klein (1982a), which paper also provides full locality data. Several female specimens of both C. streetsii and E. messinensis have been examined in the present study, from collections as documented in Von Vaupel Klein (1984). Figures and photographs shown herein have been taken from slide preparations of the furcae of two individuals, viz.:

Chirundina streetsii, ♀ spm. no. 1, 4-xi-1982, from "Dana" Exped. sta. 3782^{ii}; and
Euchirella messinensis, ♀ spm. no. 1, 9-vi-1981, from "Atlantide" Exped. sta. 139.

RESULTS AND DISCUSSION

Figure 1a presents the structure of the large, articulating setae of the furca in the female of

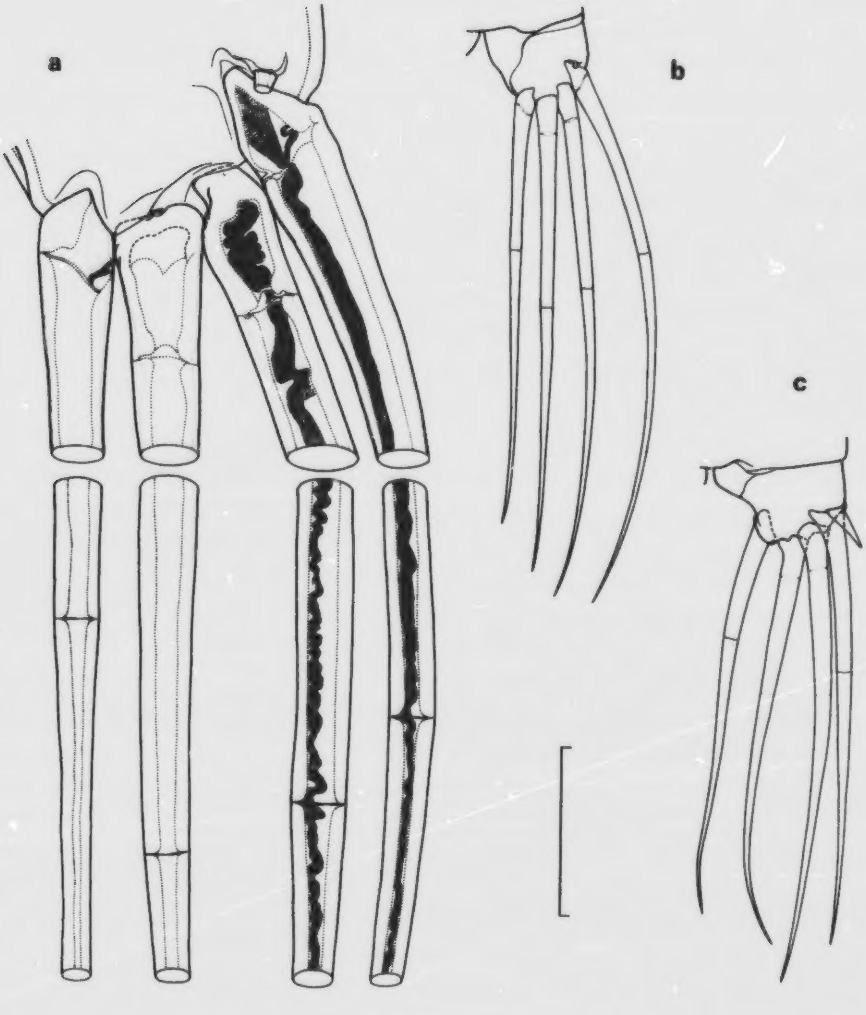

Figure 1. *Breaking planes and articulations in the four large, articulating furcal setae; hairs and setules omitted.* ***a)*** *details of (proximal) breaking planes and (distal) articulation sites in all four setae of* Chirundina streetsii *Giesbrecht, 1895, right ramus, dorsal view, with internal tissue strands shown in two lateral setae only;* ***b)*** *situation of all these (eight) modified sites on the setae of* C. streetsii*;* ***c)*** *do.,* Euchirella messinensis *(Claus, 1863), with breaking planes in intermediate setae only, and well developed articulations exclusively in the lateral and medial seta, in* ***(c)****, the sites of non-functional remnants of articulations in both intermediate setae have been indicated as well (left ramus, dorsal view, but drawn in mirror-image for comparison). Scale equals 0.1 mm for* ***a****, 0.4 mm for* ***b*** *and* ***c****.*

C. streetsii. In the two intermediate setae, a breaking plane is found at c. 0.10 the seta's length. However, in both the lateral and the medial seta, a very similarly structured region appears to be present, situated extremely proximally (Fig. 1a, b; Fig. 3a). Just like the breaking planes known from the setae of the antennae and the oral appendages, the structures found here are characterized by (1) an internal, annular sulcus in the chitinous wall of the seta, which (2) is not apparent on the outer surface, while (3) both proximally and distally of the sulcus the setal wall is distinctly thickened. This description applies in full in the case of the intermediate setae, while in both the lateral and the medial seta the configuration is not equally well developed around all of the seta's circumference, viz., being less evident in the sector adjacent to the intermediary setae, and developed most markedly in the respective sectors exposed to the environment in full.

The presence of breaking planes in the two marginal setae has, to my knowledge, not been noticed before. The references Schmeil (1892), Claus (1893), Gurney (1931), and Lang (1948) made to breaking regions in the setae of the furca, only take into account the two intermediate setae. Incidentally, the observations made earlier on the structure of these breaking planes appear to be slightly erroneous (e. g., Gurney, 1931:39, figs. 7-8; Lang, 1948:28-30). The authors cited describe breaking to take place at the breaking plane, detaching the distal part of the seta together with the proximal outer cylinder alike, from a proximal, internal stub. This phenomenon was described by Gurney (1931:39) as ".....the seta.....slips off as a glove from a finger", which assumes, in fact, the existence of a breaking cone rather than a simple breaking plane. However, the structure of the breaking plane clearly indicates that breaking at this predesigned site will involve the distal part to be detached from the complete proximal stub, the latter not being differentiated into rather independent inner and outer cylinders (e. g., Von Vaupel Klein, 1982b, fig. 4e). This assumption is confirmed by many observations of setae broken off at breaking planes, having lost the distal part only, thus retaining the complete, undivided stub in full. The phenomenon earlier observed by the above authors should, therefore, be interpreted as detachment of a whole seta at its proximal articulation with the ramus. The remaining 'stub', then, is nothing else than the torn part of the seta's core of soft, internal tissue. In the course of examining more than 40 slide preparations of furcae, the present author failed to observe anything that would corroborate the hypothesis brought forward in the presumed 'glove-effect' mechanism.

Apart from breaking planes, all four setae of a ramus show the presence of another modified site at c. 0.50 along their length (Figs. 1a, 1b, and 3b). These sites structurally resemble the articulations in the natatory setae of the legs quite strongly (cf. Von Vaupel Klein, 1982b, fig. 10f). The structure involved thus consists of (1) an internal, annular sulcus in the chitinous wall of the seta, which, however, is (2) extended throughout the entire wall so as to be observable as an irregular, tranverse suture at the setal surface (e. g., Fig. 3g), while (3), there is no thickening of the setal wall in the vicinity of the sulcus whatsoever. I hitherto failed to observe these sites in the intermediate setae of various aetideids, whereas they have been mistaken for breaking planes in both the lateral and the medial setae in some instances (cf. Von Vaupel Klein, 1982b: 17, fig. 4e).

The hydrodynamics of the urosome in the hop-and-sink type of swimming action of planktonic copepods, have been adequately outlined by Strickler (1970, 1975). The downward flap of the urosome is a powerstroke, resulting in a forwardly directed swimming movement of the animal; this implies that the upward movement is a recovery stroke. As in the case of the swimming legs (see, e. g., Strickler, 1975; Von Vaupel Klein, 1982b), obvious requirements for gaining a resulting, directional velocity component by alternating up and down movements are, that a larger force is being exerted via the bristles onto the medium (the water) in the powerstroke, than in the case of the recovery stroke. This

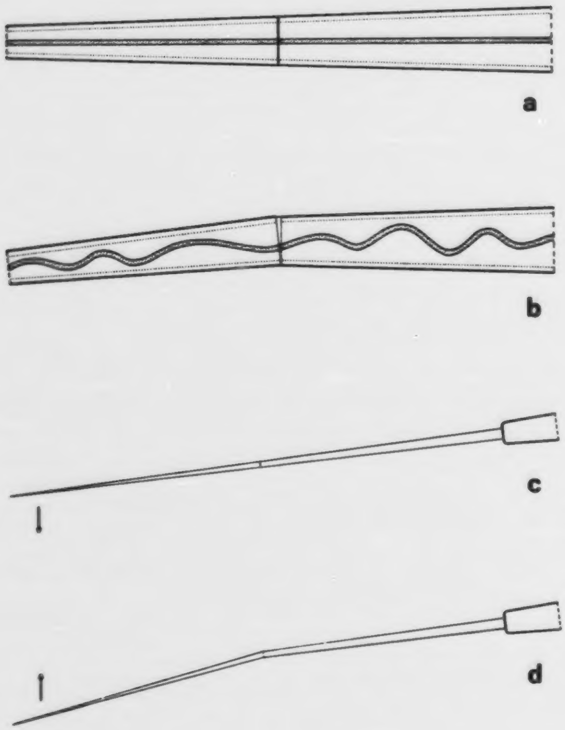

Figure 2. *Schematic representation of an articulation site allowing alternate conditions of rigidity (a) and flexibility (b) in a seta, governed by exertion c. q. relaxation of muscular action along the longitudinal axis of the seta. The mechanism as here described is presumed to be instrumental in varying the resistance of the complete seta, relative to the medium in, respectively, the powerstroke (c) and the recovery stroke (d) of the urosome in swimming performance. (All figures assume furca in right lateral view, top = dorsal, bottom = ventral, right = anterior, left = posterior).*

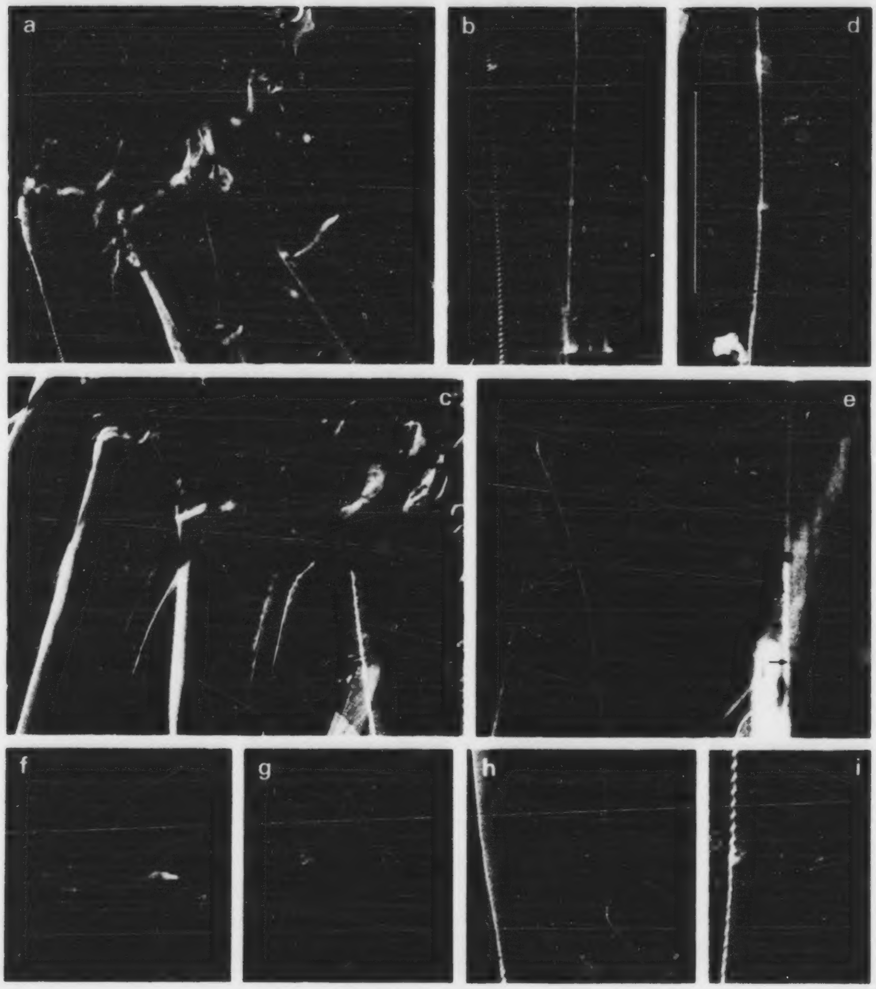

Figure 3. *Micrographs showing details of large furcal setae as observed under differential interference contrast.* ***a)*** *Chirundina streetsii Giesbrecht, 1895, caudal edge of right furcal ramus in dorsal aspect, showing breaking planes in all four setae (arrows);* ***b)*** *do., same ramus, articulation sites in lateral (right) and adjacent intermediate setae (arrows);* ***c)*** *Euchirella messinensis (Claus, 1863), caudal edge of left ramus, dorsal view, with breaking planes present in intermediate setae only (arrows);* ***d)*** *do., same ramus, articulation site in medial seta (arrow);* ***e)*** *do., same ramus, faint indications of fused articulation sites in both intermediate setae (arrows);* ***f)*** *detail of* ***(a)****, second seta from lateral;* ***g)*** *detail of* ***(b)****, second seta from lateral;* ***h)*** *detail of* ***(c)****, second seta from medial;* ***i)*** *detail of* ***(d)****. Scale of* ***(d)*** *equals 0.1 mm for* ***a-e****, 0.05 mm for* ***f-i****.*

is achieved in part by moving c. q. positioning the complete setae by muscular action (Strickler, 1975) at the main articulation seta-ramus. For another part, a stiffness-suppleness variation within the bristles themselves may be acquired by a combination of not (or: not completely) direction-limited articulations and an alternating contraction-relaxation sequence of internal muscle- c. q. tendinous fibres. A schematic representation of the principle involved is given in Fig. 2. This mechanism was suggested before for the natatory setae of the legs (Von Vaupel Klein, 1982b: 98 sqq.) and appears to apply to the furcal setae just as well.

A subsequent inspection of the furcal structures in E. messinensis learned, that the conditions in this species are quite similar, though not identical. The breaking planes in the intermediate setae directly correspond to those in C. streetsii, but in the lateral and the medial seta a proximal breaking plane as observed in the latter species is absent in E. messinensis. The articulation sites in the lateral and in the medial seta are the same in both species, but those in the intermediate setae are usually completely lacking in E. messinensis, or they may, at most, be traced as faint, transverse ripples, apparent remnants of now fused, former articulation sites. The relative positions of all structures, as far as present, are remarkably similar in both species and thus would indicate a homologous inheritance from some common ancestor. This observation, of course, excludes the breaking planes in the marginal setae of C. streetsii, no indications of which could be traced in E. messinensis. An undoubtedly interesting survey of the occurence of breaking planes and articulation sites will be incorporated in my ongoing review of aetideid calanoids and I hope colleagues working on other free-living copepods will report their observations of these structures in due course.

A summary of possible functional demands in the various regions of the furcal setae is presented in table 1, along with the sites at which these may actually be located. **Positioning** the seta (as a whole), is presumed to be restricted to the articulation of the seta with its supporting ramus. Active differentiation in stiffness vs. suppleness resulting in **passive articulation**, may be performed both at this articulation as well as at the midway articulation sites. **Passive detachment** of (part of) the seta may, as a consequence of reduced robustness, take place preferentially at all three sites under concern, i. e., at the articulation with the ramus, at the predesigned breaking plane, or at the distal articulation site. In this case, the actual occurrence of all three possibilities can be witnessed in regular observations of preserved material. Finally, **autotomy**, if it occurs at all, seems to be restricted to the breaking plane proper, as judged from the absence of relevant muscular configurations at the other two types of modified sites. In the case of the breaking plane the condition of the preserved material did not allow a conclusive answer as to be possible presence of autotomous structures, while obviously a study on this phenomenon has to employ sectioning techniques as well.

Table 1. *A comparison of functions and their locations among the various modified large furcal setae of calanoids*

	Function			
	Active positioning	**Passive articulation**	**Passive detachment**	**Active autotomy**
Site:				
Articulation with ramus	+	+	+	-
Breaking plane	-	-	+	(+)
Articulation site	-	+	+	-

In conclusion it may be noted, that a remarkably similar mechanism apparently serves the hydrodynamics of the swimming performance in both the setae of the natatory legs and those of the furca. Such observations might well be considered as pleading once more in favour of the origin of the furcal rami as a modified pair of appendages (i. c., uropods; see Bowman, 1971), rather than a metameric formation of the trunk (e. g., Claus, 1863; Hartog, 1888; for a review see Lang, 1948).

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Mr. J. Simons and his staff (Zoological Laboratory, State University at Leiden) expertly printed the photographs and my wife, Pauline, kindly typed the manuscript. Their assistance is gratefully acknowledged.

Note added in proof: As regards the use of the term 'breaking planes', Dr. B.M. Marcotte (McGill University, Montreal, Canada), lately pointed out to me, that in fact 'fracture planes' would be more correct. I thus intend to employ the latter term in future publications.

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THE ZOOGEOGRAPHY OF THE GENUS PSEUDODIAPTOMUS (CALANOIDA: PSEUDODIAPTOMIDAE)

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Abstract: Pseudodiaptomids are primarily demersal in habit, found from freshwater to coastal marine waters, and circumglobal in distribution. These calanoids generally migrate into the water column at dusk and remain near or attached to bottom substrates during the day. The 70 species in the genus Pseudodiaptomus are divided into 7 morphologically, though not necessarily geographically, distinct species groups. Morphological variations in the fifth pair of legs of males are used for species determination. About 35 species are present in the eastern Indo-Pacific, 23 in the western Indo-Pacific, 15 in the Americas, 6 in Japanese waters, and 5 species along southern African waters. Allopatry, sympatry, and parapatry are expressed within these species groups.

Recent plankton studies using emergence traps or diver-towed nets near the bottom, have yielded new species and distributional information on several demersal calanoids (Alldredge and King, 1980; Ohlhorst, 1982; Barr, 1984; Walter, 1984). Members of the genus Pseudodiaptomus inhabit fresh to hypersaline waters, in most tropical and temperate coastal areas, and display a pronounced diel migration.

In the genus Pseudodiaptomus, species and species groups can be distinguished primarily by the presence or absence of endopods (Ri) on the right and left male fifth legs (P5), with the female P5 and habitus of both the male and female serving a secondary role in species determination (Walter, unpubl. data). The 70 known species, 39 of which I have examined, may be divided into 7 species groups (Table 1).

Table 1: *Characteristics for Pseudodiaptomus species groups and species subgroups assemblages. IP = Found in Indo-Pacific; A = Found around southern half of Africa; B = Found in North and/or South American waters; F = Reported from freshwater habitats; S = Schmackeria according to Marsh, 1933; U = Specimens deposited at USNM; X = Reported only once in literature; O = Only female reported in the literature; NA = No available or unclear illustrations in the literature.*

	IP	A	B	F	S	U	X	O	NA
1) NUDUS									
1) P. clevei Scott, 1909	+	-	-	-	-	+	-	-	-
2) P. gracilis (Dahl, 1894)	-	-	+	+	-	+	-	-	-
2) AMERICANUS									
A) "acutus-subgroup"									
3) P. acutus (Dahl, 1894)	-	-	+	-	-	+	-	-	-
4) P. acutus leptopus Loeffler, 1963	-	-	+	-	-	-	-	-	-
5) P. galapagensis Grice, 1964	-	-	+	-	-	+	-	-	-
6) P. richardi (Dahl, 1894)	-	-	+	+	-	+	-	-	-
7) P. richardi inequalis (Brian, 1926)	-	-	+	+	-	-	+	-	-
8) P. wrighti Johnson, 1964	-	-	+	-	-	+	+	-	-
B) "pelagicus-subgroup"									
9) P. americanus Wright, 1937	-	-	+	-	-	-	+	-	-
10) P. cokeri González and Bowman, 1965	-	-	+	-	-	+	-	-	-
11) P. coronatus Williams, 1906	-	-	+	-	-	+	-	-	-
12) P. cristobalensis Marsh, 1913	-	-	+	-	-	-	-	-	-

Table I (continued)

	IP	A	B	F	S	U	X	O	NA
13) P. culebrensis Marsh, 1913	-	-	+	-	-	-	-	-	-
14) P. euryhalinus Johnson, 1939	-	-	+	-	-	+	-	-	-
15) P. marshi Wright, 1936	-	-	+	-	-	+	+	-	-
16) P. pelagicus Herrick, 1884	-	-	+	-	-	?	+	-	-
3) BURCKHARDTI									
17) P. burckhardti Sewell, 1932	+	-	-	-	-	+	-	-	-
4) IMPROCERUS									
18) P. adamanensis Pillai, 1980	+	-	-	-	-	-	-	-	-
19) P. batillipes Brehm, 1954	-	+	-	-	-	-	+	-	-
20) P. charteri Grindley, 1963	-	+	-	-	-	-	-	-	-
21) P. hessei (Mrazek, 1894)	-	+	-	-	-	-	-	-	-
22) P. pauliani Brehm, 1951	-	+	-	-	-	-	+	-	-
23) P. stuhlmanni (Poppe and Mrazek, 1895)	-	+	-	-	-	-	+	-	-
24) P. sp. 1	+	-	-	-	-	+	-	-	-
5) LOBUS									
A) "forbesi-subgroup"									
25) P. annandalei Sewell, 1919	+	-	-	+	+	+	-	-	-
26) P. binghami Sewell, 1912	+	-	-	+	+	-	-	-	-
27) P. binghami malayalus Wellershaus, 1969	+	-	-	+	-	+	-	-	-
28) P. brehmi Keifer, 1938	+	-	-	+	-	-	+	-	-
29) P. bulbosus (Shen and Tai, 1964)	+	-	-	+	-	-	+	-	-
30) P. forbesi (Poppe and Richard, 1890)	+	-	-	+	+	-	-	-	-
31) P. inflatus (Shen and Tai, 1964)	+	-	-	+	-	-	+	-	-
32) P. inopinus Burckhardt, 1913	+	-	-	+	+	-	-	-	-
33) P. inopinus saccupodus (Shen and Tai, 1962)	+	-	-	+	-	-	+	-	-
34) P. lobipes Gurney, 1907	+	-	-	+	+	-	-	-	-
35) P. poplesia (Shen, 1955)	+	-	-	+	-	-	-	-	-
36) P. spatulatus (Shen and Tai, 1964)	+	-	-	+	-	-	+	-	-
B) "poppei-subgroup"									
37) P. poppei Stingelin, 1900	+	-	-	+	+	-	+	-	-
38) P. smithi Wright, 1928	+	-	-	+	+	+	+	-	-
39) P. tollingeri Sewell, 1919	+	-	-	+	+	+	-	-	-
6) HYALINUS									
A) "aurivilli-subgroup"									
40) P. aurivilli Cleve, 1901	+	-	-	-	-	+	-	-	-
41) P. bowmani Walter, 1984	+	-	-	-	-	+	-	-	-
42) P. compactus Walter, 1984	+	-	-	-	-	-	-	-	-
43) P. mertoni Fruchtl, 1923	+	-	-	-	-	+	-	-	-
B) "trihamatus-subgroup"									
44) P. baylyi Walter, 1984	+	-	-	-	-	+	-	-	-
45) P. bispinosus Walter, 1984	+	-	-	-	-	+	-	-	-
46) P. incisus Shen and Lee, 1963	+	-	-	-	-	-	+	-	-
47) P. sewelli Walter, 1984	+	-	-	-	-	-	-	-	-
48) P. trihamatus Wright, 1937	+	-	-	-	-	+	-	-	-
49)?P. dauglishi Sewell, 1932	+	-	-	+	-	?	-	-	-
7) RAMOSUS									
A) "serricaudatus-subgroup"									
50) P. ardjuna Brehm, 1953	+	-	-	-	-	-	-	-	-
51) P. sp. 2	+	-	-	-	-	+	-	-	-
52) P. hickmani Sewell, 1912	+	-	-	+	-	-	-	-	-
53) P. sp. Nishida (pers comm)	+	-	-	-	-	+	-	-	-
54) P. jonesi Pillai, 1970	+	-	-	-	-	+	-	-	-
55) P. marinus Sato, 1913	+	-	-	-	-	+	-	-	-
56) p. serricaudatus (T. Scott, 1894)	+	-	-	-	+	+	-	-	-
B) "salinus-subgroup"									
57) P. sp. 3	+	-	-	-	-	+	-	-	-
58) P. colefaxi Bayly, 1966	+	-	-	-	-	+	-	-	-
59) P. cornutus Nicholls, 1944	+	-	-	-	-	+	-	-	-
60) P. sp. 4	+	-	-	-	-	+	-	-	-
61) P. galleti (Rose, 1957)	+	-	-	-	-	+	-	-	-
62) P. nihonkaiensis Hirakawa, 1983	+	-	-	-	-	+	-	-	-
63) P. sp. 5	+	-	-	-	-	+	-	-	-
64) P. salinus (Giesbrecht, 1896)	+	-	-	-	-	-	-	-	-

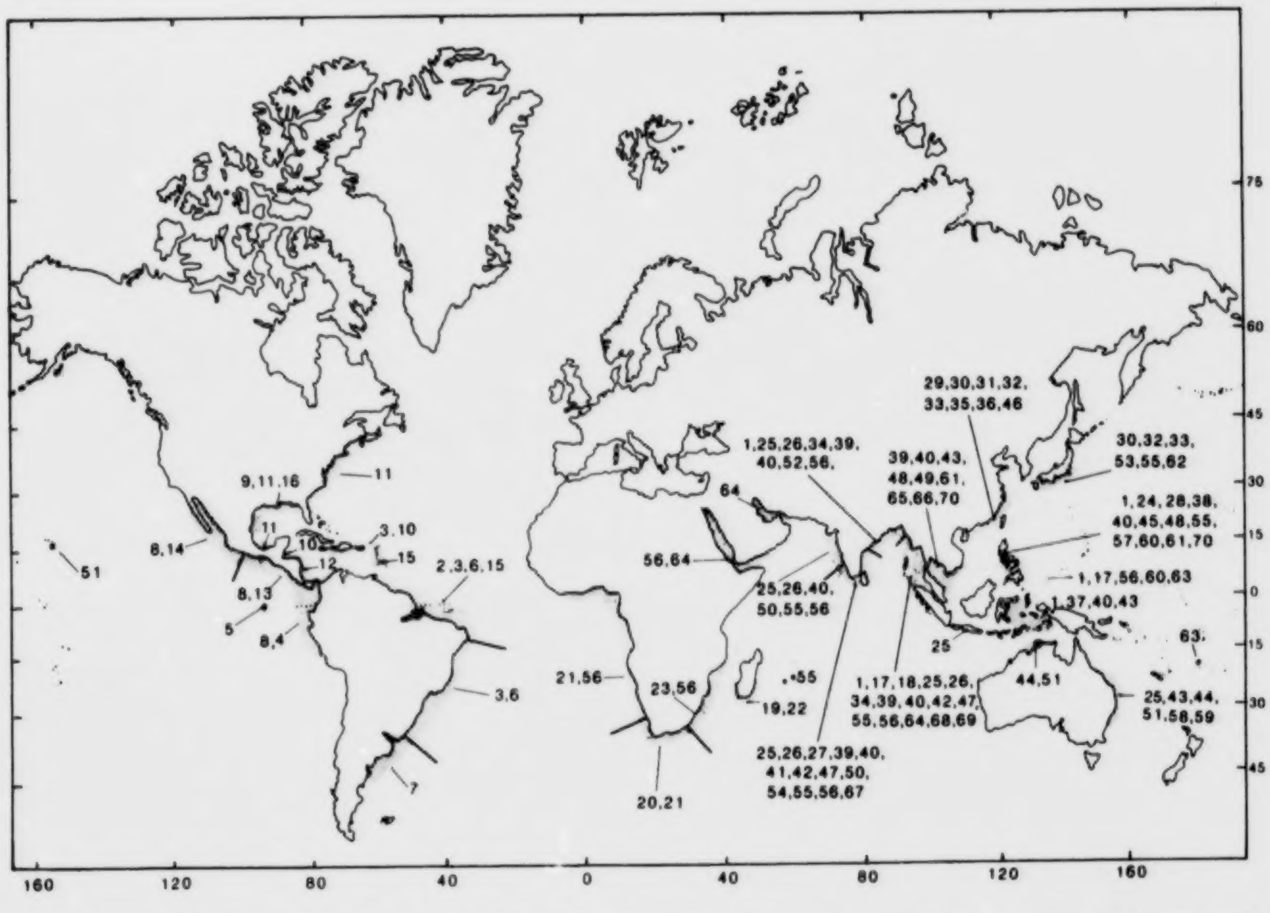
Table 1 (continued)

	IP	A	B	F	S	U	X	O	NA
8) DUBIOUS UNASSIGNED SPECIES									
65) *P. beieri* Brehm, 1951 [= ?*P. dauglishi*]	+	-	-	-	-	-	-	-	+
66) *P. bulbiferus* (Rose, 1957)	+	-	-	-	-	-	-	+	-
67) *P. heterothrix* Brehm, 1953	+	-	-	-	-	-	-	-	+
68) *P. masoni* Sewell, 1932	+	-	-	-	-	-	-	+	-
69) *P. nankauriensis* Roy, 1977	+	-	-	-	-	-	-	+	-
70) *P. ornatus* (Rose, 1957)	+	-	-	-	-	+	-	+	-

Fifty species have been reported from the Indo-Pacific region (Figure 1), most of them collected from coastal brackish water to marine habitats (coral reefs, coral rubbles, grassbeds, river mouths, mud embayments, fishponds, and mangroves). Several Indo-Chinese species (particularly of the Lobus group) occur in predominantly freshwater habitats (rivers, inland lakes and reservoirs); most species in this group were assigned by Marsh (1933), who had no Indo-Pacific material to examine, to the genus *Schmackeria* Poppe and Richard, 1890. I concur with Wright (1936), Vervoort (1965), and Pillai (1980) that *Schmackeria* is a synonym of *Pseudodiaptomus*. Some species display a distinctly euryhaline character such as two American species (*P. coronatus* and *P. euryhalinus*) and two African species (*P. charteri* and *P. hessei*), the latter pair being pioneer species that quickly establish dense populations after estuarine flooding (Wooldridge and Melville-Smith, 1979).

Fourteen species (Americanus group) are endemic to both coasts of North and South America, with all species lacking a right Ri on the male P5. Herrick (1884) described *P. pelagicus*, the type-species of the genus, from brackish waters of the Mississippi Sound. Unfortunately, no material was deposited and this species has not been reported again. However *P. coronatus* Williams, 1906, which has strong morphological affinities to *P. pelagicus*, has been regularly reported from these waters. I have examined pseudodiaptomids from Maine, Massachusetts, Virginia, North and South Carolina, Florida, Louisiana, Texas and Mexico and have found only *P. coronatus*. I consider *P. coronatus* a synonym of *P. pelagicus* because of the close morphological similarities of both species (particularly the male P5), the presence of only 1 species on the Atlantic coast and Gulf of Mexico, and the fact that Williams (1906) made no reference to Herrick's work. Only two species, *P. euryhalinus* and *P. wrighti* have been reported from the west coast of North America. The former is unique among pseudodiaptomids in that the female has only 2 instead of the typical 3-4 urosomal segments. Since the reviews of Marsh (1933) and Wright (1936), four new Central-South American species have been reported. After examining most of the known species from North America south to Argentina and Ecuador, I have divided the Americanus species group into 2 subgroups (Table 1), with members of both assemblages present in both Atlantic and Pacific coastal waters. In his review of Argentinian copepods, Ringuelet (1958) synonymized *P. richardi emancipans* Brehm, 1957 with *P. richardi inequalis*. The only other American pseudodiaptomid known is *P. gracilis* (Nudus group) reported from the lower Amazon basin. This species is unique among the American species in that it lacks both a left and right Ri on the male P5 and possesses lateral head hooks. A possible allopatric counterpart to *P. gracilis* is the marine Indo-Pacific *P. clevei*, however, the latter lacks lateral head hooks.

Along the coast of western and southern Africa are found *P. hessei*, *P. charteri*, and *P. stuhlmanni* of the Improcerus species group. Another species, *P. serricaudatus* of the Ramosus group also co-occurs in this region, but extends around north to the Red Sea. Other reports of *P. serricaudatus* (Mori, 1942; Vervoort, 1965; Wellershaus, 1969) from Indian waters east to the Palau Islands gives this species the most extensive geographical range among pseudodiaptomids. *Pseudodiaptomus salinus* was originally


75
60
45
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41,42,47,50,
54,55,56,67
39,40,43,
48,49,61,
65,66,70
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34,39,40,42,47,
55,56,64,68,69
29,30,31,32,
33,35,36,46
30,32,33,
53,55,62
1,24,28,38,
40,45,48,55,
57,60,61,70
1,17,56,60,63
1,37,40,43
25
44,51
63
25,43,44,
51,58,59

Figure 1. *Worldwide distribution of species in the genus* *__Pseudodiaptomus__. The numbers refer to species listed in Table 1.*

described from the Red Sea and Arabian Sea area; recently, I have observed it from samples taken in the Persian Gulf. Around the island of Madagascar two poorly known species P. pauliani and P. batillipes have been reported but once in the literature.

In the west Indo-Pacific region 16 species of Pseudodiaptomus, representing 3 species groups (Table 1), are reported from the coastal waters of India. Previous reports of P. mertoni from Indian waters are actually misidentifications of the species P. bowmani, P. sewelli, and P. compactus (Walter, 1984), with P. mertoni restricted to the southern half of the east Indo-Pacific region. The surrounding waters of the Nicobar-Andaman Island chain appear to be the crossroads to the east Indo-Pacific with 15 species known representing 6 species groups.

Along the coastal areas of Malaysia, Thailand, and Viet Nam (east Indo-Pacific region), there occur 3 species groups including 9 species, of which 3 species are common to the Nicobar-Andaman Island vicinity. Further north, a unique assemblage of morphologically distinct species is recorded from China. All but one of these species, P. incisus of the Hyalinus group, were collected from freshwater habitats and are of the Lobus group. From Japan, the northern-most reported area for pseudodiaptomids, 6 species have been reported from 2 species groups. At present there are 12 species, representing 5 species groups, known from the Philippines with ten of these species being marine and collected by emergence plankton traps from one locale (Walter et al., 1982; Walter, 1984; Walter, unpubl. data). The other 2 species were reported from inland lakes on the islands of Luzon and Mindoro. Further east, 5 species (P. burckhardti, P. clevei, P. serricaudatus, P. sp. 4, P. sp. 5) are known from the Palau Islands (Mori, 1942; Walter, unpubl. data). Since P. clevei and P. sp. 4 co-occur in Philippine waters, the other Palau species may eventually be found in these waters. The coastal areas of Papua New Guinea, Aru Archipelago, and the north-eastern coasts of Australia are home to 9 species from 4 species groups.

Previous attempts to divide the genus (Sewell, 1924; Marsh, 1933; Pillai, 1980) into distinct assemblages have not been entirely successful. The euryhaline nature of pseudodiaptominds led Sewell (1958) to place species into 3 groups based on salinity tolerances (fresh, brackish, and/or marine waters). Members of the Lobus group are predominantely freshwater in habit, but occasionally some are reported from the marine environment. The other groups are recorded from brackish to marine waters and only occasionally enter freshwater habitats, with the Hyalinus and Ramosus groups dominated by marine forms. The present arrangement of species groups and subgroups, based primarily on sexually modified structures on the male P5, appears valid for the genus as a whole, as all species with known males can be assigned to one of the groups.

Although faunal centers of planktonic taxa are difficult to determine, the Indo-Malayan region appears to be the center of speciation for Pseudodiaptomus. The areas of greatest diversity, with 5 and 6 species groups respectively, are the Philippine and Nicobar-Andaman Archipelagos. The co-occurrence of as many as 10 sympatric species of a genus from one locale, such as those collected by the author from the Philippines, is not regularly reported for calanoids. Species diversity declines with increasing distance from the faunal center, appearing lowest along the African and Arabian coastlines. This reduction in diversity may in part be the result of undercollecting. Species previously thought to range from Japan to Australia are separable into series of closely related species (Walter, unpubl. data). Further studies of demersal zooplankton should produce new records and species, allowing better elucidation of phylogenetic relationships and zoogeographical distribution of pseudodiaptomids.

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VARIABILITY OF DIAPAUSE IN COPEPODS

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Abstract: Diapause in many marine and freshwater copepods often takes place under conditions which appear favourable for continued growth and development of the population involved. While termination of diapause has frequently been recognized as the primary factor synchronizing actively growing stages with favourable growing conditions, the initiation of arrest appears to cut down on the potential for free growth and development.

Laboratory rearings indicate that induction of diapause results from an interaction of daylength and temperature which the individual copepod interprets as a signal to continue development or enter arrest. Differences in opinion exist about mechanisms which allow the variable responses which occur in populations in different localities.

One of the features of diapause in copepods is the variability of response which populations in different waterbodies demonstrate. A sampling of this variability is shown in Table 1. Two major patterns can be observed; either there is considerable difference in the life-history pattern of a species along a latitudinal gradient, or life-histories vary in different sized waterbodies in the same locality. These differences result from differences in intensity and persistence of diapause and I postulate they result from a flexible response to gradients of both photoperiod and temperature. This flexible approach could be the best strategy for copepods, because diapause is a drastic developmental alternative which may be necessary for survival but which brings with it considerable disadvantages, such as extension of development time, potentially increased mortality and restriction of growth to only part of the year.

Table 1: *Examples of copepod species whose life cycles differ in different regions or in different waterbodies in the same region. (Presumably these differences result from diapause in one or more generations in some populations.)*

I Latitudinal gradients in life cycles:

a) Mesocyclops leuckarti - continuous development in subtropical lakes; winter diapause in Italian Lakes; absent in winter in English Lake District. Smyly (1961).

b) Calanus finmarchicus - continuous development south of English Channel; Multivoltine with summer diapause, Firth of Clyde; Single generation, developing in spring, Norwegian fjords. Grigg and Bardwell (1982), Tande (1982).

c) Labidocera aestiva - continuous development, Florida coast, summer development, Virginia; absent winter to spring, Delaware and north. Marcus (1984).

II Different life cycles in waterbodies in the same region:

a) Diacyclops thomasi - Laurentian Great Lakes, Lake Erie summer diapause; Lake Ontario continuous development. Watson (1974).

b) Cyclops strenuus and Cyclops scutifer - Various life-history patterns in small ponds to larger deeper lakes, Norway. Elgmork (1980).

c) Diaptomus sanguineus - different life-cycles and numbers of generations from permanent and temporary ponds. Hairston and Olds (1984).

Diapause appears to be a mechanism for avoiding the control of environmental factors when neither growth nor development are temperature or food controlled. Various authors have demonstrated that food intake is restricted, and that metabolism is low and requires very little oxygen (see Watson and Smallman, 1971b, for references). Energy requirements in this "torpid" state are low and apparently are supplied by the conversion of glycogen reserves to lipid. Survival over long periods with sparse food in this state may represent a net energy saving in comparison to an actively metabolizing, starving, individual. Transition of stored reserves to lipid may provide those copepods which spend late juvenile or adult stages in diapause with readily available energy reserves for the deposition of several clutches of eggs after arrest is terminated. Drastically lowered oxygen requirements allow survival in waters of low oxygen tension, and changes in behaviour allow relatively torpid animals to sink to levels in the water or sediments where predation is less.

These behavioural and metabolic changes inherent in diapause tend to compensate for losses in production and increases in mortality due to the extended duration of life, and provide a means of escape from unfavourable conditions.

The interactive nature of photoperiod and developmental temperature in initiating diapause has been demonstrated by Watson and Smallman (1971a) and Marcus (1982). When reared under some combinations of these two factors, individuals from the same population all develop to maturity, while at other combinations all will enter diapause. An intermediate range of conditions produces a varying proportion of animals which enter diapause. Thus the critical photoperiods which are usually cited in the literature represent the daylength at which 50% of the population enter arrest.

While Watson and Smallman (1971a) report critical photoperiods for two species of temporary pond cyclopoids, this information does not offer much insight into how the species manage to survive the temporary pond situation where they live, or how their diapause responses allow them to appear at different times of year. The observations that one species enters diapause when exposed to days shorter than certain values, and the other does so when exposed to days longer than given values are more useful in understanding the basic pattern of occurrence.

In addition temperature was shown to modify the entry of each species into diapause. In one case, low temperature increased the proportion of cyclopoids entering diapause at a particular daylength while the reverse was true for the other species. This is evident from the shifts in critical photoperiod which occurred when rearings were made at different temperatures.

This laboratory information is borne out by field observations of seasonal distribution of the two species. Both were found in the same temporary woodland ponds in south-eastern Ontario. These ponds were dry in summer and flooded in late fall. Diacyclops "A" was found as a winter, early-spring dominant replaced in mid-April to early May by D. navus. This later species produced a generation, at least part of which entered arrest, before the ponds dried up in June. Although neither species was present all the time that the ponds were flooded, the photoperiod and temperature responses of both were such that periods of active development coincided with the presence of water in the pools, and diapausing individuals were produced to carry each species over periods of summer drought. In this case at least, the unique responses to photoperiod modified by temperatures of these two species can be used to explain their seasonal distribution more effectively than a definition of critical photoperiods alone. Therefore it seems quite feasible to develop an ecological classification of copepod diapause types based on the types of responses to photoperiod and temperature observed in these two species. This would be similar to a classification for insects developed by Danilevskii (1965).

Based on these findings two responses are possible; either short or long days initiate diapause;

similarly, there are two temperature effects: either low or higher temperatures enhance processes leading to diapause.

If these effects of photoperiod and temperature are independent, it is possible to combine responses to them into four categories. These are listed in Table 2.

Table 2: *Four potential types of diapause/development response based on observed reactions to a combination of photoperiod and temperature (possible life-cyle patterns in mid-latitude temperate waters which would result from such interactions and examples are suggested).*

Type I	Days shorter than a particular value induce diapause; low temperatures enhance diapause. (Diapause occurs in late fall continues through winter, development resumes late spring). Likely example: Labidocera aestiva: Marcus (1982); Diacyclops navus, this paper.
Type II	Days shorter than a particular value induce diapause; low temperatures enhance continuous development. (Diapause would occur in late summer, continue through winter, development would resume early spring). Possible example: Mesocyclops leuckarti, Smyly (1961).
Type III	Days shorter than a particular value allow continuous development; low temperatures enhance diapause. (Diapause would occur in late spring, continue through summer, development would resume in early fall). Possible example: Cyclops strenuus, Elgmork (1980).
Type IV	Days shorter than a particular value allow continuous development; low temperatures enhance continuous development. (Diapause occurs in summer, continues through fall, development resumes in winter). Likely examples: Calanus finmarchicus, Grigg and Bardwell (1982). Diacyclops "A", this study.

Two of the postulated categories of response have already been observed in rearings of the two species of Diacyclops. These typify two extremes of development pattern. In the first, (Type I of Table 2), copepods enter diapause on exposure to short days with lower temperatures enhancing the response. In a Type IV response, short days and low temperature cause copepods to develop directly, while longer days and higher temperatures cause them to enter diapause.

Species demonstrating the two other types of response suggested in Table 2 have not been investigated as yet in the laboratory, but observed developmental patterns in the field suggest likely candidates for each of these types.

Looking at the responses of different species in this way offers an insight into the ecology of co-existing species and explains an advantage of diapause recently suggested by Marcus (1984). Related species, such as the two species of Diacyclops described above, with different developmental responses to photoperiod and temperature may be able to partition a restricted habitat temporally rather than spatially, and thus cut down on competition for food or other resources. It would be interesting to study the swarm of morphologically similar sibling species identified by Price (1958) in the nominal species Acanthocyclops vernalis s. lat. in this regard, because some forms are known to co-exist in the same temporary or permanent ponds over a wide geographic range.

This analysis suggests that considerable flexibility can be developed in the seasonal induction (and probably termination) of diapause at a particular time of year among species of copepods by combining pairs of alternative responses to photoperiod and temperature. For each species the degree of diapause within a local population, and hence the observed seasonal life-history pattern in that locality, can be predicted as a response to these environmental stimuli.

Besides the seasonal variability which exists at any place in photoperiod and temperature there is also a latitudinal gradient of photoperiod and temperature at most times of year. This should produce different patterns of diapause response along the gradient. Within any local region where daylengths are identical, temperature differences can easily exist between different aquatic habitats for a variety of reasons including morphometric differences, different water masses etc. Here, temperature modifications of photoperiodic effects should create different diapause responses.

This interpretation of diapause as a flexible response to prior environmental signals, resulting in different proportions of populations entering arrest at different times of year in different localities is borne out by laboratory surveys where temperature and photoperiod were varied over a wide range of conditions. Other authors who have examined field populations come to different conclusions, which suggest that local populations are closely adapted to specific conditions.

Marcus (1984) and Hairston and Olds (1984) consider that the proportion of copepods which enter arrest in a given locality is genetically controlled by selection of critical photoperiods matched to the pressures of the environment. Marcus points out that this would lead to the development of a large number of potentially isolated populations. Hairston and Olds consider that these populations should be finely adapted to their local environment. While there is unquestionably a genetic basis to the control of diapause, the evidence from the two species of Diacyclops studied by Watson and Smallman (1971a) indicates that there is considerable flexibility in the physiological basis of diapause control within single local populations. This should also be true over the range of a species, and should maintain the potential for interbreeding and maintaining the flexibiltiy.

Further studies are needed to determine the mechanisms which allow the diapause responses of copepods to be so closely related to the diverse environmental conditions they experience.

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Posters

RELATIONSHIP OF MOUTHPART STRUCTURE AND FOOD IN COPEPODS FROM THE COLLECTION OF THE FIRST BRAZILIAN ANTARCTIC EXPEDITION (1983)

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Abstract: The plankton samples were taken in Jan. 83 at several stations extending from latitude $60^{\circ}48'$S to $64^{\circ}36'$S and longitude $52^{\circ}58'$W to $64^{\circ}34'$W. The plankton was collected by a Bongo net and samples from 300 um mesh were analysed.

The following species were recorded: *Calanus propinquus*, *Calanus tonsus*, *Calanoides acutus*, *Rhincalanus nasutus*, *R. gigas*, *Clausocalanus laticeps*, *Ctenocalanus citer*, *Euchaeta antarctica*, *Scolecithricella glacialis*, *Metridia gerlachei*, *M. lucens*, *Oithona similis*, *O. plumifera* and *Oncaea conifera*. The most abundant and frequent species are in order of importance: *Ctenocalanus citer*, *Metridia gerlachei*, *Calanus propinquus* and *Calanoides acutus*.

With the help of photos and drawings of the material collected an attempt is being made to understand the niche partition of available food for the different species and different stages of copepods.

INTRODUCTION

Much has been published on the ecological rôle of the Euphausiacea in the Antarctic waters while that of the planktonic copepods has been sorely neglected. However, here, as in any marine ecosystem, copepods play an important rôle as primary consumers.

An attempt is made here to establish the relationship between the structure of the mouthparts of the surface water copepods and size of the available food, using the material collected by the First Brazilian Antarctic Expedition.

MATERIAL AND METHODS

Phytoplankton and zooplankton were simultaneously collected in the Bransfield Strait, January 1983 (Fig. 1). Zooplankton samples were collected from the upper 150 m with a Bongo net (mesh size 330 um). Filtering mesh-size of the maxillary setae of the copepods was measured under the microscope and the lowest values were considered. Average total sizes of the copepod species are given.

RESULTS

The copepod population in the Antarctic waters surveyed in the present study was composed of 15 species (Tab. 1). The small calanoid *Ctenocalanus citer* Bowman and Heron ranks first in numerical abundance, followed by *Calanus propinquus* Brady and *Calanoides acutus* (Giesbrecht). Both of the latter species are about equally abundant.

Rhincalanus gigas Brady and *R. nasutus* Giesbrecht ahve low density and a patchy occurrence in surface waters, compared to those of *Calanus propinquus*, *Calanoides acutus* and *Ctenocalanus citer*.

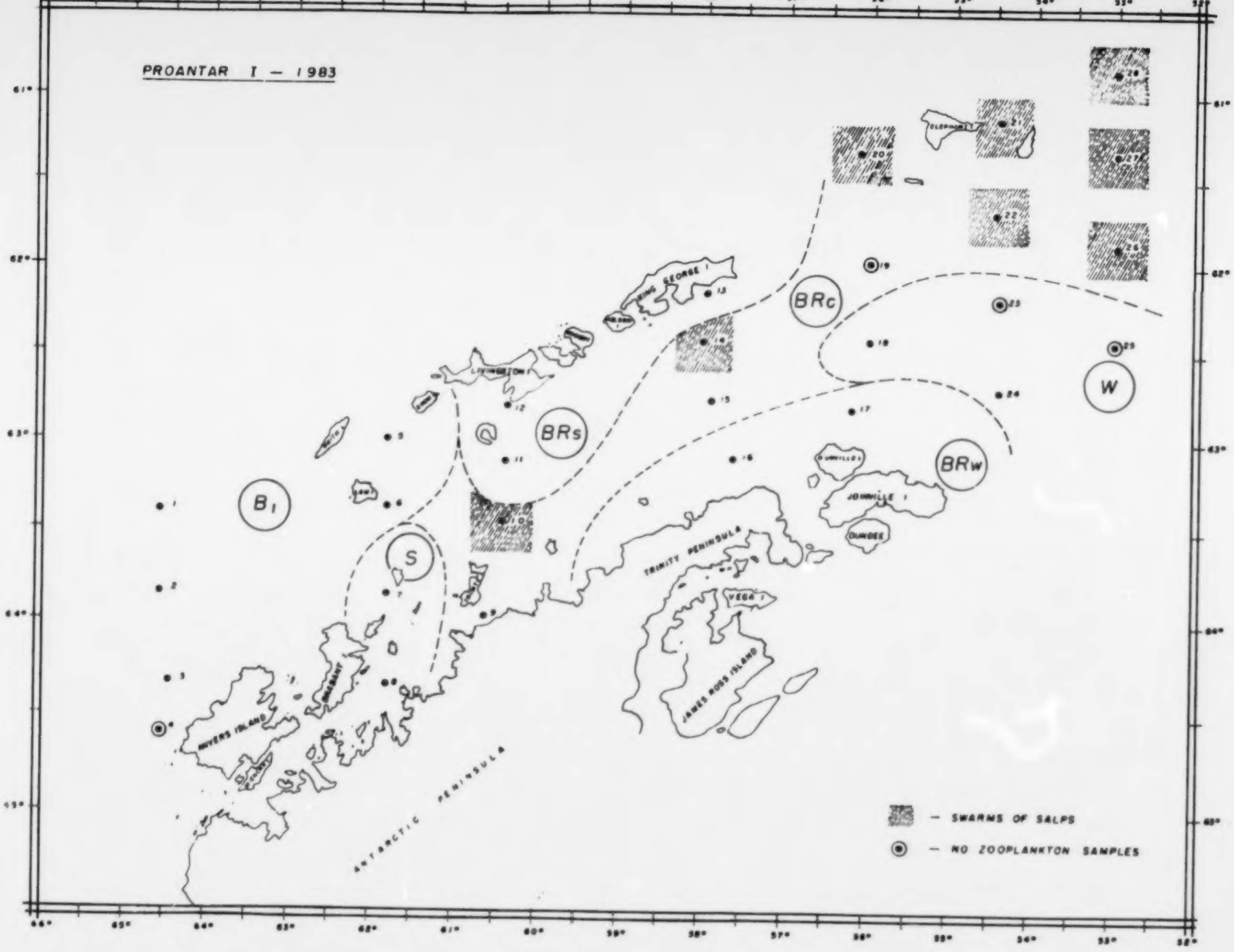
PROANTAR I – 1983
B1
S
BRs
BRc
BRw
W
KING GEORGE I.
LIVINGSTON I.
ELEPHANT I.
JOINVILLE I.
DUNDEE
VEGA I.
TRINITY PENINSULA
JAMES ROSS ISLAND
ANVERS ISLAND
BRABANT I.
ANTARCTIC PENINSULA
– SWARMS OF SALPS
– NO ZOOPLANKTON SAMPLES

Figure 1. *Map of stations (B_1, S, BR_S, BR_C, BR_W, W - watermasses, from Ikeda et al., 1983).*

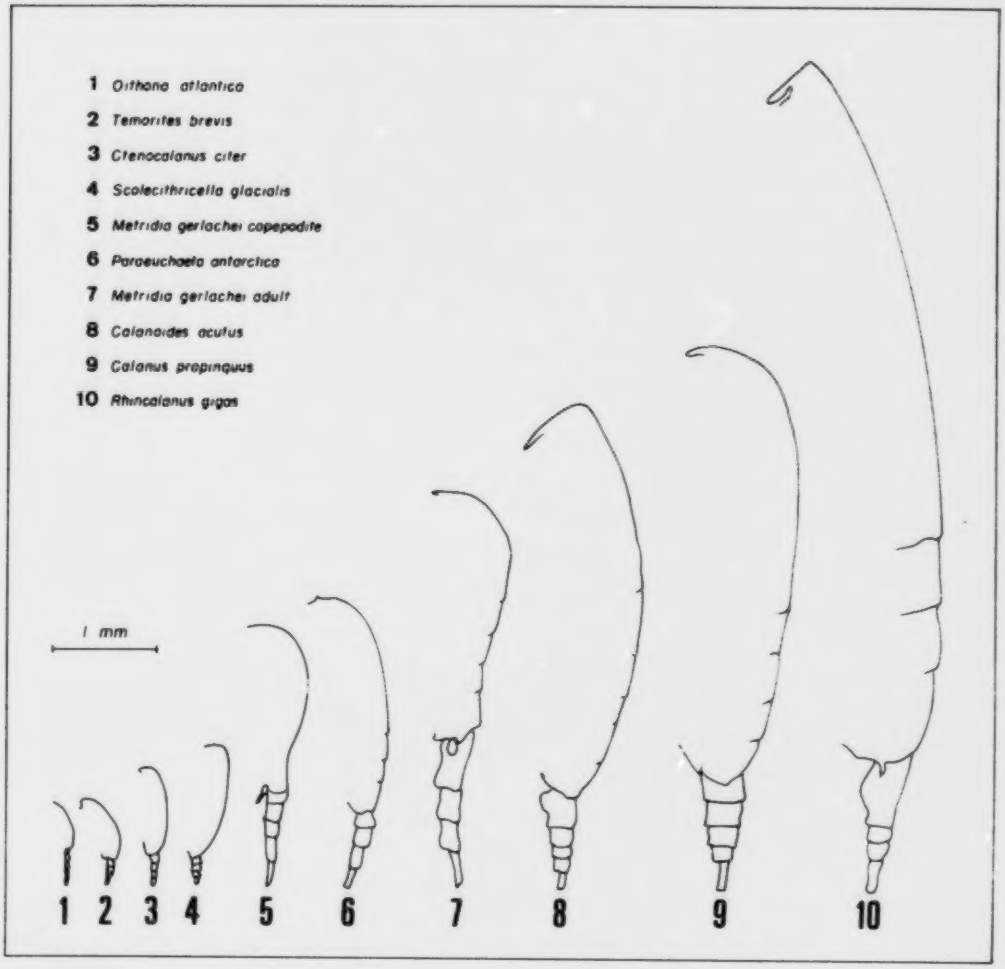
1 Oithona atlantica
2 Temorites brevis
3 Ctenocalanus citer
4 Scolecithricella glacialis
5 Metridia gerlachei copepodite
6 Paraeuchaeta antarctica
7 Metridia gerlachei adult
8 Calanoides acutus
9 Calanus propinquus
10 Rhincalanus gigas
1 mm
1
2
3
4
5
6
7
8
9
10

Figure 2. *Outlines, indicating sizes of the different copepod species found.*

Table 1. *Stations see Figure 1*

Species/Stations	1	2	3	5	6	7	8	9	10	11	12	13	14	15	16	17	18	20	21	22	24	26	27	28
Calanus propinquus	83	75	1	26	14	10	197	60	2	26	-	128	29	8	20	7	44	22	15	53	9	26	1	32
Calanoides acutus	5	31	5	10	10	12	264	34	-	7	23	138	-	2	15	51	45	5	51	23	3	2	-	7
Rhincalanus gigas	8	1	2	1	-	-	-	-	-	2	-	4	-	1	-	-	13	-	-	1	-	-	-	1
Rhincalanus nasutus	15	18	6	2	4	-	-	-	-	2	-	2	-	2	2	-	2	-	-	3	-	2	-	2
Ctenocalanus citer	153	195	239	99	14	6	288	163	2	1	2	3	14	5	7	138	89	206	2	942	25	34	1	15
Clausocalanus laticeps	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	35	-	-	-	-	-	-	-
Paraeuchaeta antarctica	73	3	3	6	2	3	5	1	-	1	-	27	6	20	8	29	-	2	-	1	6	1	-	1
Racovitzanus antarcticus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3	2	-	10	3	1	-	17
Scolecithricella glacialis	35	18	5	12	5	1	2	1	-	-	-	-	49	15	12	-	3	-	-	-	-	2	-	-
Temorites brevis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	42	9	-	-	-	21	-	-	-
Metridia gerlachei	613	14	-	-	2	-	-	34	-	-	-	3	442	14	12	76	42	4	-	3	30	6	-	-
Metridia lucens	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oithona atlantica	8	-	-	1	3	-	7	6	-	-	1	-	-	-	17	66	47	-	-	52	12	-	-	10
Oithona similis	-	-	5	4	-	2	3	6	-	-	-	-	-	-	-	20	-	1	-	8	3	2	-	1
Oncaea conifera	-	-	-	-	1	-	3	2	-	-	-	-	-	-	1	9	2	1	-	-	4	-	-	1

However, these species have a wide vertical distribution, unlike the first three species which have an even distribution in the surface water. Clausocalanus laticeps Farran occurs only occasionally. The unspecialized filter feeders ("omnivores") have a patchy distribution; Metridia gerlachei Giesbrecht is most abundant, followed by Scolecithricella glacialis (Giesbrecht) and Oithona atlantica Farran. Only a few specimens of Paraeuchaeta antarctica Giesbrecht, Racovitzanus antarcticus Giesbrecht, Temorites brevis Sars, Metridia lucens Boeck, Oithona similis Claus, and Oncaea conifera Giesbrecht were found.

Large swarms of salps, probably Salpa thompsoni Foxton, occurred in our collection, especially in the "BR_C" water mass (see Fig. 1 and Ikeda et al., 1983). When salps were abundant, the density of copepods was always very low.

The copepods reported here can be divided into two different size groups (Fig. 2). The first group is composed of very small calanoids, of less than 2 mm in total length, markedly dominated by Ctenocalanus citer. The second group of larger calanoids is not dominated by any particular species.

Species like Oithona atlantica, Temorites brevis and Scolecithricella glacialis with more omnivorous mouthparts are included among the small species; they are probably filter feeders due to the scarcity

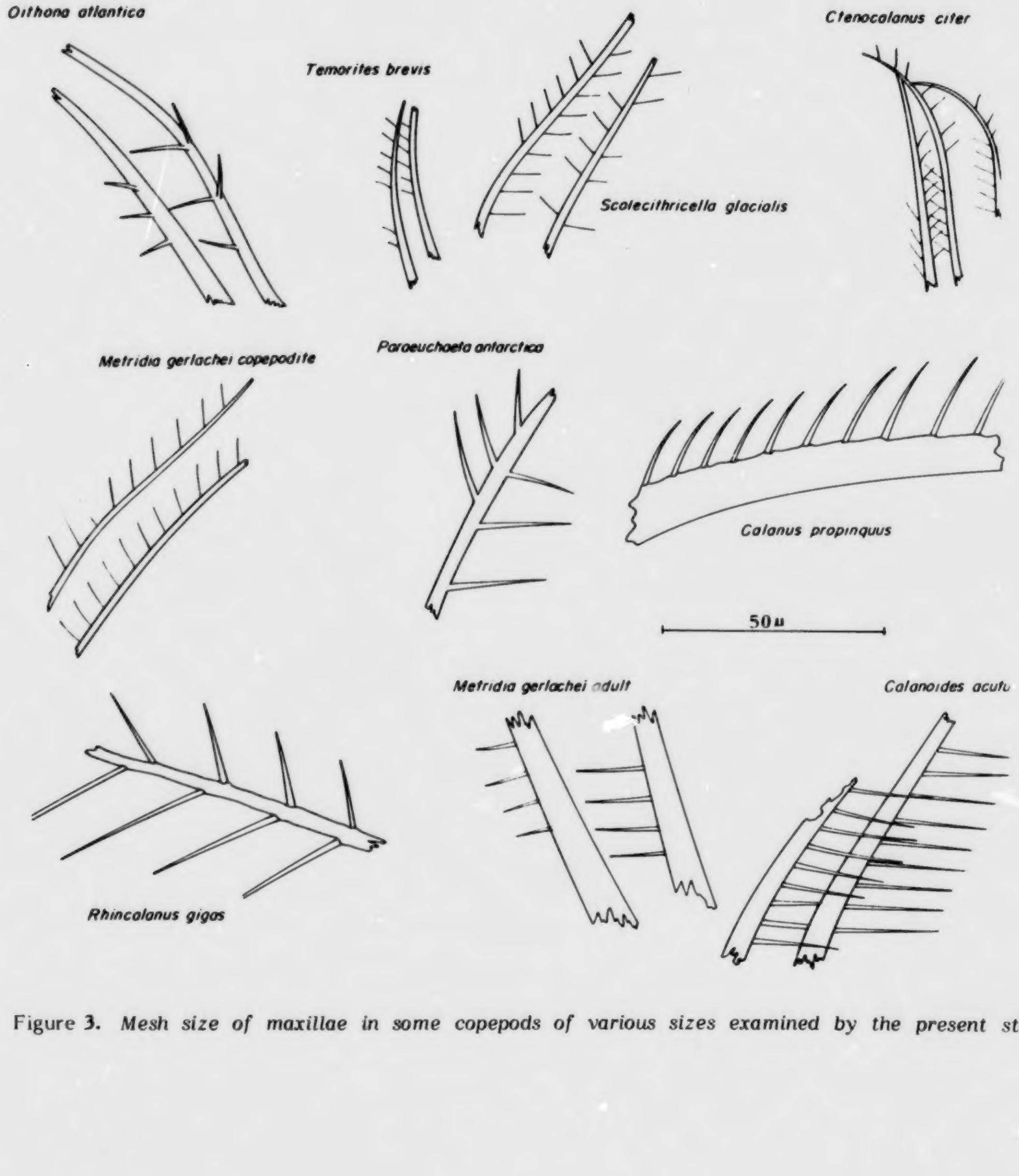
Oithona atlantica
Temorites brevis
Scolecithricella glacialis
Ctenocalanus citer
Metridia gerlachei copepodite
Paraeuchaeta antarctica
Calanus propinquus
50 μ
Metridia gerlachei adult
Calanoides acutu
Rhincalanus gigas

Figure 3. *Mesh size of maxillae in some copepods of various sizes examined by the present study.*

of detritus in the Antarctic waters.

There is a positive relation between the body size and the filtering mesh size of the maxillae (Fig . 3) (The cyclopoid Oithona does not fit in the series). The small copepods have a mesh size range of 1-2 μm and the larger copepods of 7-14 μm. Thus the food particles in the range of 2-7 um are not effectively utilized by filter feeding copepods (Fig. 4). It is assumed that food particles in this size range are exploited by other filter feeders in the zooplankton, such as young euphausiids and copepodids of the larger copepods. The salps probably compete with copepods in the small particle range.

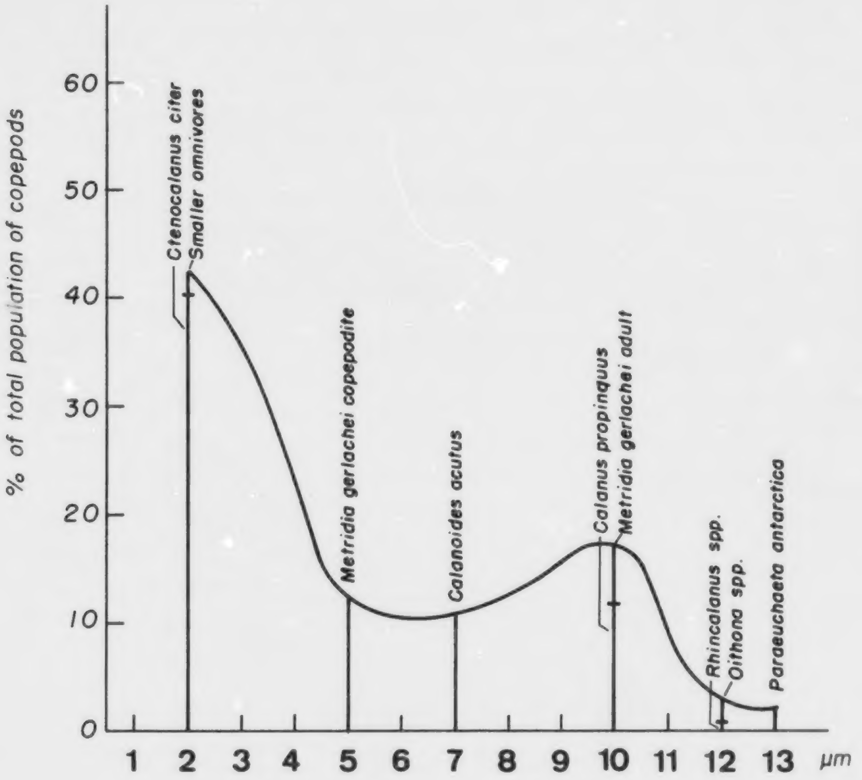

Figure 4. *Total number of copepods in the samples, expressed in percentage per species and arranged according to increasing filtrating mesh-size.*

DISCUSSION

The bimodal distribution of the filtering mesh size of the maxilla in the epiplanktonic copepods in the Antarcitc waters seems to correspond to the bimodal distribution of the microflagellates in the same area found by Brandini and Kutner (pers. comm.). They noted that the most abundant fractions of flagellates are those of 1-3 um and 6-10 um. The cell counts of the flagellates in the range of 3-6 um are, on average, only half or less than those in the other two categories. Copepods with a filtering mesh size around 12-13 um probably feed on dinoflagellates and diatoms.

It should be noted that the body size of *Ctenocalanus citer* is about one-fifth that of the large filter feeders such as *Calanus propinquus*. One may assume that the small species matures and reproduces, however, faster than the large species.

The basically circumpolar distribution of the copepod assemblage to which the present fauna belongs has been emphasized by Baker (1956) and Vervoort (1957) among others. Most copepod studies dealt with the large species, but recently Kaczmaruk (1983) has emphasized the importance of the small copepods, such as *Ctenocalanus citer* and *Oithona* spp., in the Antarcitc waters. The present study confirms the numerical dominance of *C. citer* in the Antarctic surface waters. The importance of this species has previously been unnoticed because of the large mesh size of nets used.

Lately, increasing attention has been given to the nannoplankton producers. It appears that species of the genus *Ctenocalanus* are among the most important nannoplankton filter feeders in marine environments (Almeida Prado Por, 1983).

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STUDIES ON MARINE COPEPODS BY CHINESE SCIENTISTS DURING THE LAST 35 YEARS

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Abstract: Marine Copepoda researches has made a marked progress, particulary in the taxonomy field in China for the past 35 years. A series of scientific surveys on marine Copepoda along our coast were organized by Academia Sinica, Administration of Fisheries and National Bureau of Oceanography, etc. Many new species were established. Based upon the species identified, together with their zoogeographical and ecological studies in different species and related to fisheries were also carried out by our scientists. The results of these studies are also discussed in the present paper.

This report is a brief account of the progress in the study of marine copepods by Chinese scientists during the last 35 years. Several Chinese institutions, including the Chinese Academy of Sciences, Adminstration of Fisheries, National Bureau of Oceanography, and a number of laboratories attached to universities and fisheries colleges have sponsored taxonomic, biological, fisheries, and other studies on copepods of the adjacent seas of China, including the Yellow Sea (the Gulf of Bohai included), the East China Sea, the South China Sea, and western Pacific (Fig. 1).

TAXONOMIC AND FAUNISTIC STUDIES

Taxonomic studies of copepods of the Yellow Sea were carried out by Shen and Bai (1956), Chen and Zhang (1965), Chen, Zhang and Zhu (1974), and Lian and Lin (1983), the East China Sea by Shen (1955), Chen and Zhang (1965), Chen, Zhang and Zhu (1974), and Lian and Lin (1983), and the South China Sea by Shen and Lee (1963), Shen and Tai (1964), Chen and Shen (1974), Chen and Zhang (1974), Chen B. (1982), and Chen Q. (1983). A total of 400 species have been reported from the adjacent seas of China. There are 27 species known from the Gulf of Bohai, 35 from the northern Yellow Sea, 92 from the southern Yellow Sea, 225 from the East China Sea, 199 from the Taiwan Strait, 125 from the coastal area along eastern Taiwan Province, nearly 400 from the South China Sea, and 243 from the western Pacific.

Thirty new species have been reported: Schmackeria poplesia and Tortanus vermiculus by Shen (1955); Paracalanus intermedius, Tortanus spinicaudatus, Cyclopina heterospina, Hemicyclops dilatatus, Parameira pendula, and P. brevifurca by Shen and Bai (1956); Paracalanus serrulus, Centropages brevifurcus, Labidocera sinilobata, Pontella tridactyla, Acartiella sinensis, Pseudodiaptomus incisus, and Tortanus denticulatus by Shen and Lee (1963); Sinocalanus laevidactylus, Pseudodiaptomus bulbosa, P. spatulata by Shen and Tai (1964); Paracalanus gracilis, Xanthocalanus multispinus, Scolecithricella longispinosa, Stephos pentacanthos, Centropages sinensis, Pontella sinica, P. latifurca, and Tortanus dextrilobatus by Chen and Zhang (1965); Pontellopsis inflatodigitata and Calocalanus monospinus by Chen and Shen (1974); and Tortanus sinensis by Chen Q. (1983).

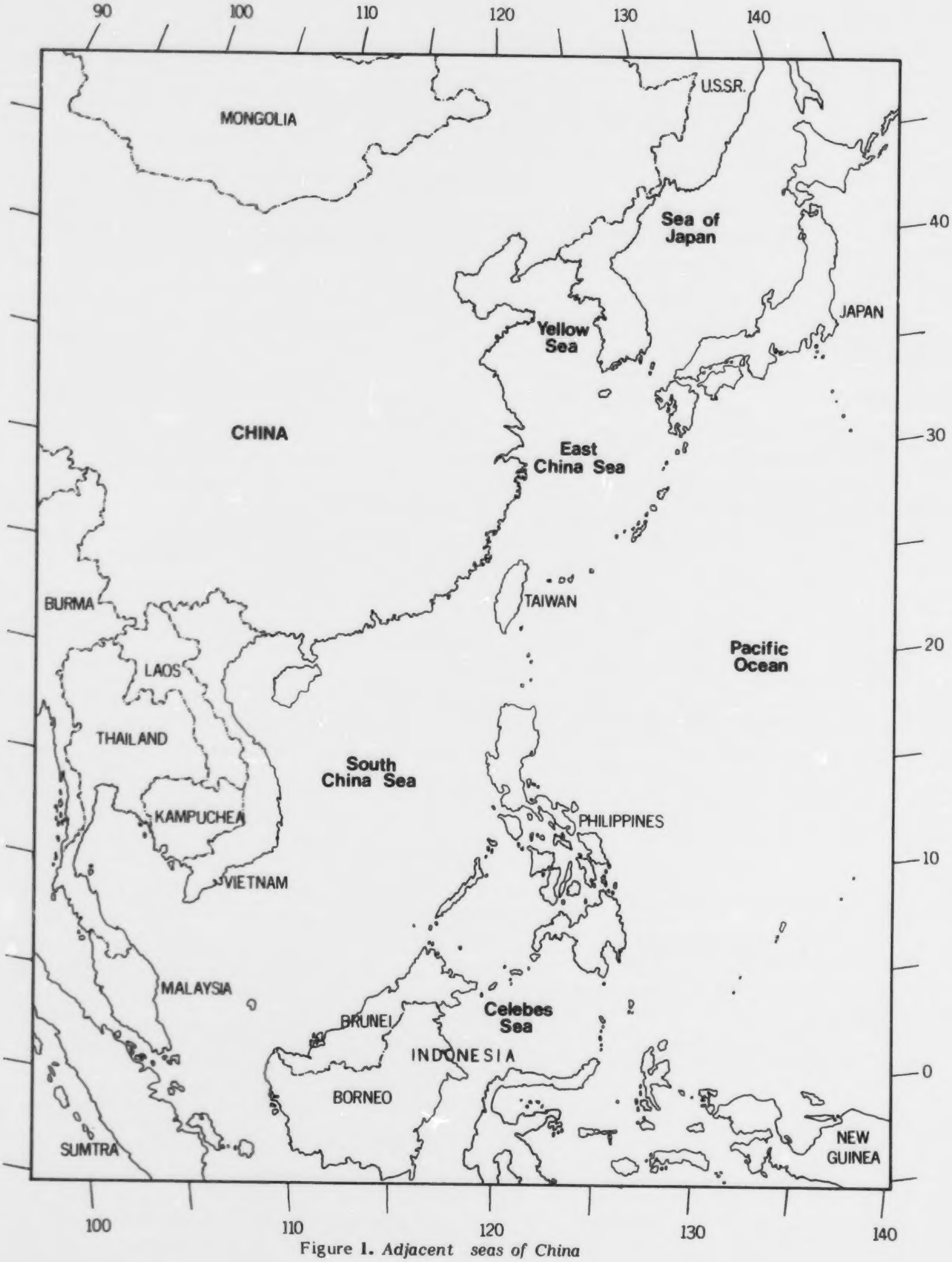
90
100
110
120
130
140
U.S.S.R.
MONGOLIA
Sea of Japan
40
JAPAN
Yellow Sea
CHINA
East China Sea
30
BURMA
TAIWAN
LAOS
Pacific Ocean
20
THAILAND
South China Sea
KAMPUCHEA
PHILIPPINES
10
VIETNAM
MALAYSIA
Celebes Sea
BRUNEI
INDONESIA
0
BORNEO
SUMTRA
NEW GUINEA
100
110
120
130
140

Figure 1. *Adjacent seas of China*

Based on surveys carried out by various Chinese institutions, it has been noted that the copepod fauna in the Gulf of Bohai and the Yellow Sea is dominated by warm-temperate species. In the East China Sea east of 123°E where it is strongly influenced by the warm current Kuroshio and in the South China Sea, tropical species prevail. A transitional area is located between 29° and 32°N and west of 123°E in the East China Sea where the warm-temperate and tropical faunas mix (Chen, Chen and Hu, 1982).

DISTRIBUTIONAL STUDIES

Based on the distributional pattern, copepod species of the adjacent seas of China may be divided into two groups: one that occurs in coastal waters with low salinity and a wide range of water temperature, such as *Labidocera euchaeta*, *Paracalanus crassirostris* (Chen and Zhang 1965); and the other that inhabits offshore water with high salinity and small range of water temperature, e.g., *Pleuromamma gracilis*, *Rhincalanus cornutus* (Chen Q., 1982).

The abundance for each copepod species varies with area and season. *Calanus sinicus*, *Paracalanus parvus*, and *Centropages mcmurrichi* are most abundant in the Yellow Sea in July (Chen and Zhang, 1965) and *Undinula vulgaris* and *Euchaeta subtenuis* in the South China Sea from June to September (Chen Q., 1982).

Quantitative vertical distribution of copepods seems to be relatively stable throughout the year. In deep water stations, the center of abundance both in biomass and in species diversity is usually in the upper 100 m layer, frequently an aggregation of copepods is found within the depth of 40-60 m (Chen, Zhang and Chen, 1978; Chen Q., 1982).

Some copepod species perform diurnal vertical migration. The general pattern of this diurnal migration varies from species to species and from one stage to another in the life history of the same species. In general four patterns are recognizable (Chen, Chen and Zhang, 1978; Chen, 1982):

1. Descending at midnight and ascending at dawn as in *Eucalanus elongatus*, *Calanus sinicus* and *Euchaeta concinna*.
2. Ascending during the day and descending at night as in *Corycaeus* spp.
3. Irregular migration as in *Temora discaudata*, *Centropages gracilis*, and *Calanopia thompsoni*.
4. Weak vertical migration as in *Calocalanus pavo*, *Pontella fera*, and *Labidocera detruncata*.

BIOLOGICAL STUDIES

Feeding habit of several species of copepods have been reported (Lee, 1964). *Paracalanus parvus* and *Temora turbinata* are non-selective plant feeders. *Centropages tenuiremis* and *Acartia pacifica* are omnivores with preference for plant rather than animal diet. *Euchaeta concinna* and *Tortanus derjuginii* are carnivores. A close relationship between feeding habits and the structure of mouth-parts is found in these species.

Ingestion and absorption of food by copepods have been observed with ^{14}C ($NaH^{14}CO_3$) or ^{35}S (^{35}S-Methionine) labelling techniques. In studying *Schmackeria dubia*, Huang and Luo (1980) found that the filtering rate, feeding rate, and absorption rate increase markedly with development of the animals.

The absorption efficiency decreases with the increase of the food density, and remains at a lower level in further raising of the food density. It seems that superfluous feeding may be encountered in higher level of food density.

Based on collection from the Gulf of Bohai to the South China Sea, Chen Q. (1964) studied the breeding periods, sex ratio, and variation in body size of a common calanoid species, Calanus sinicus. This species breeds three times a year in the Yellow and the East China seas in March to May, June to August, and October to November but only once in the South China Sea in early spring. The ratio of female to male in copepodite V is 1:1 but females far exceed males in number in the adult stage throughout the year. Variation in the size of adults varies with area and season but apparently closely related to temperature. There is a marked decrease in size of the adults of this species from north to south.

The life cycles of some common calanoids species of Xiamen (Amoy) Harbour were studied from specimens taken in plankton samples as well as live animals reared in the laboratory by Li and Fang (1983a, 1983b, 1984). Based on an analysis of the abundance of different developmental stages, the percentage distribution of the instar stages, and the sizes of adults, they concluded that there are nine, six, and five generations per year respectively for Labidocera euchaeta, Temora turbinata, and Centropages tenuiremis. They also found that L. euchaeta does not feed in the naupliar stage and its sexual dimorphism first appears at copepodite IV. The development of naupliar and copepodid stages of Calanus sinicus is very similar to that of C. helgolandicus (Li and Fang, 1983 c). The sexual dimorphism of the former first appears at copepodite V.

The effects of temperature on the development of copepods have also been studied. Chen S. (pers. comm.) reared a coastal copepod, Euterpina acutifrons, in the laboratory under two temperature conditions. When reared at 25.6-30.8°C (summer temperature), the duration of time for this species from hatching to maturation is 3-9 days and at 7.6-18.3°C (winter to spring temperature), 12-16 days. Zheng and Tian (pers. comm.) found for a rock pool harpacticoid, Tigriopus japonicus, that the breeding, life span, and fecundity is significantly affected by low temperature condition.

Chen J. (pers. comm.) and Li and Yan (pers. comm.) respectively studied the effects of Cu^{++} and Hg^{++} on the fecundity of Acartia pacifica under controlled laboratory conditions. A similar response of daily egg production to these ions was found. The number of eggs produced by each female is inversely proportional to the concentration of these ions in the medium.

Lipid content of copepods in offshore deep waters is usually higher than that of other planktonic crustaceans in nearshore waters. In contrast, protein, amino acid and carbohydrate contents of copepods are generally greater than those in deeper waters (Lin, pers. comm.). The carbon content of planktonic copepods is the highest among all planktonic crustaceans (Chen and Zhang, unpublished data).

FISHERIES STUDIES

Copepods are the dominant group of zooplankton in the fishing grounds. Calanus sinicus, Centropages mcmurrichi, Corycaeus affinis, Paracalanus parvus and Acartia clausi are abundant in the Yelow and East Chinas Seas, and Undinula vulgaris, Euchaeta marina, Temora turbinata, Scolecithrix danae, Eucalanus subtenuis, and Acartia pacifica in the South China Sea. These copepods form the major food items of the mackerel, Pneumatophorus japonicus, and scad, Decapterus maruadsi. The abundance of copepods and the productivity of a fishing group are positively related. For instance, schooling of fish takes place in the southeastern part of the East China Sea in late autumn when warm current, Kuroshio, brings in a large quantity of warm water copepods to this area (Chen Y. et al., 1980).

Cheng and Fang (1956, 1957) studied the feeding habits of two planktivorous fishes, Coilia grayii and C. mystus. They found these fishes feed mainly on planktonic crustaceans which are dominated by copepods, especially Paracalanus parvus, Pseudodiaptomus marinus, and Tortanus forcipatus.

Copepods are fished in some parts of China for human consumption and poultry industry. In the tributaries of the Pearl River in Guangdong Province, the commercial copepod fishery has a history of more than a century. The fishing season is from November to February. Copepods are caught with large stationary nets set in sounds where tidal currents are of moderate strength. The catches are usually best during late evening and at night when copepods ascend to the surface. The annual catch is about 1,500 metric tons. In the day of Xianshan of Zhejiang Province, Centropages mcmurrichi is fished in spring.

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*As a rule, the family name of a Chinese author precedes his/her given name in publications published in the People's Republic of China, e.g., Chen (family name) before Boyun (given name). In quoting a reference of these publications in a text, the family name of the author(s) should be used, e.g., Chen (1982). In case of several references with authors of the same family name and the same publication date, it is advisable to cite the family name and initial, e.g., Chen B. (1982) and Chen Q. (1982).

SEX-ASSOCIATED TRANSLOCATION HETEROZYGOSITY IN CYCLOPOID COPEPODA

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Abstract: Female meiosis in cyclopoid copepods is achiasmate. Two species of cyclopoids viz: Mesocyclops edax $2n = 14$ and Acanthocyclops vernalis $2n = 4$ show translocation heterozygosity. The frequency of heterozygotes is so high that their maintenance by positve selection for translocation heterozygosity seems likely.

It is suggested that the complex structural heterozygosity seen in these cyclopoid species is sex-linked, since the fixation of heterozygosity by sex association allows time for the accumulation of adaptive gene combinations in the translocation complexes.

A considerable variety of sex-determining mechanisms are known in Crustacea. Bisexual reproduction is the rule in this class. But at least in two families in the subclass Cirripedia, hermaphroditism is found in most species. It occurs sporadically in some other groups of Crustacea (White, 1973).

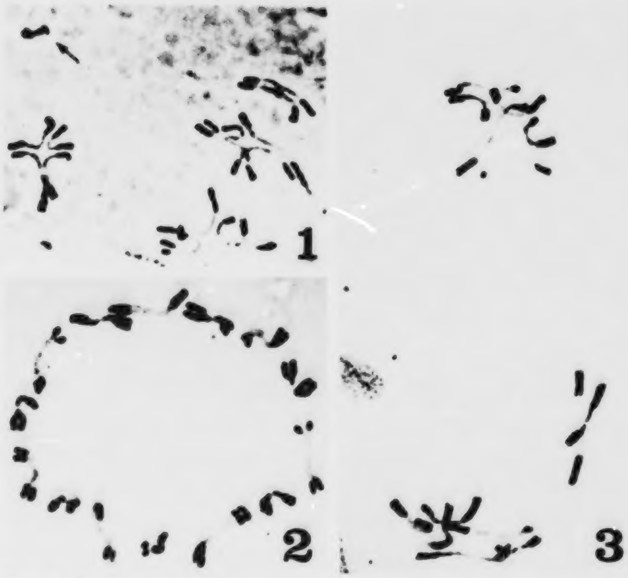
The cytogenetics of cyclopoids is remarkable in serveral respects. Unusual features already established include achiasmate meiosis in female (Matschek, 1910; W. Beermann, 1954; S. Beermann, 1977; Rüsch,1960; Chinnappa and Victor, 1979), chiasmate meiosis in male (S. Beermann, 1977), diverse sex chromosome mechanisms such as 00, X0 and XY types (W. Beermann, 1954; Rüsch, 1960; Ar-Rushdi, 1963; S. Beermann, 1977; Chinnappa and Victor, 1979), complex heterozygosity in female (Chinnappa and Victor, 1979; Chinnappa, 1980), variation in heterochromatin content and size of chromosome sets at diploid level, as well as size difference in haploid sets (S. Beermann, 1966, 1977).

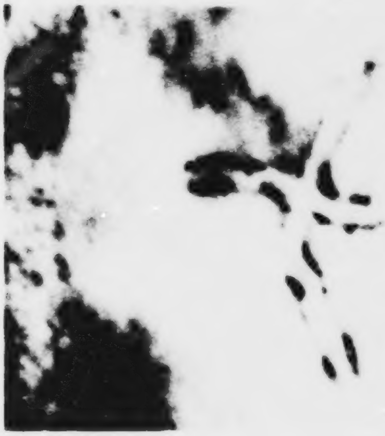
In Mesocyclops edax the females consistently show multivalents at meiosis, ranging from a ring of 4 to 6, 8, 10, 12 and 14 (Figs. 1-3; also see Wyngaard and Chinnappa, 1982). In a number of cases the frequencies of heterozygotes in a population are so high (Table 1), that their maintenance by positive selection for translocation heterozygotes seem likely. In another cyclopoid Acanthocyclops vernalis s.l. ($2n = 4$), from Broadacre Lake, North Carolina, U.S.A., the females always had a ring of four chromosomes at meiosis (Fig. 4).

Table 1. *Frequency of Occurence of Female Heterozygotes in Seven Populations of Mesocyclops edax.*

	Banister Lake Ontario, Canada	Gulf Lake Ontario, Canada	Long Lake Ontario, Canada	Heart Lake Ontario, Canada	Douglas Lake Michigan, U.S.A.	Lake Thonotosassa Florida, U.S.A.	Fairy Lake Florida, U.S.A.
% Heterozygotes	100	100	30	100	91	17	72

Translocations should have a role in the evolution of sex chromosome mechanism, in bringing the non-allelic factors into close linkage. In the simplest case of sex determination involving two loci on





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Figures 1-3. Mesocyclops edax 2n = 14. Diakinesis, female meiosis. (X900).

1. One bivalent and three rings with four chromosomes in each ring. Arrow indicates a B-chromosome.
2. Ring of 14 chromosomes.
3. One bivalent and two rings with six chromosomes in each ring.

Figure 4. Acanthocyclops vernalis 2n = 4. Pachytene pairing in a translocation heterozygote. (X2300).

different chromosomes, a reciprocal translocation involving these two pairs of chromosomes would bring the genes into linkage, and generate a sex-associated ring of four. If this linkage was achieved indirectly through an intermediate translocation, a sex-associated ring with higher number of chromosomes is accomplished. This would be a sex-linked translocation complex. The genes for sex determination should occur on the same chromosome, with no crossing-over between loci, so that particular chromosomes become indentified with sex determination. Perhaps the fixation of translocation heterozygosity by sex association allows time for accumulation of adaptive gene combinations in the translocation complexes. Such complexes would have more likelihood of being conserved than exchanges directly exposed to selection.

Sex-linked translocation heterozygosity has been reported for the calanoid copepod Diaptomus castor (Matschek, 1910; Heberer, 1932). In the oogonial meiosis a ring of six chromosomes in addition to 14 bivalents were observed. The males had 17 bivalents and no rings. All the mechanisms of sex-chromosome complex heterozygosity in animals are confined to one sex, they differ from Oenothera plant system in that no balanced lethals or "Renner effects" are involved. White (1973) has argued that the adaptive value of such systems is the fixation of a great deal of genetic heterozygosity even though it occurs in one sex. Since female meiosis in cyclopoids is achiasmate, it is likely that some species have evolved to stabilize permanent translocation heterozygosity. Translocations, therefore, conserve large linkage groups in which adaptive gene complexes can accumulate by natural selection. Since individuals which are translocation heterozygotes may have slightly reduced fertility, depending on the frequency of adjacent chromosome segregation at meiosis, the selection pressure favoring these animals must be relatively strong. It is difficult to understand why special mechanisms which boost genetic heterozygosity are necessary. The explanation probably lies in the ecology and reproductive biology of the species. The two cyclopoids referred here viz: Mesocyclops edax and Acanthocyclops vernalis, are indeed two of the most successful and widely distributed species in North America.

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BIOMASS ESTIMATION OF TEMORA LONGICORNIS ON THE BASIS OF GEOMETRIC METHOD

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Abstract: Among the quantitative zooplankton studies for estimation of biomass in the Baltic, the geometric measurements of 893 specimens of the different copepodid stages of Temora longicornis were carried out from Gdańsk Bay and Słupsk Trough.

Volumes and weight was calculated according to a formula proposed by Chojnacki (1980) and for determination of length-weight relationship the formula $W = AL^B$ (Huxley, 1932) was used. The general formula of total length (L_t) and weight relationships of Temora longicornis for two regions of the southern Baltic was $W = 0.274\ L_t\ 2.746$.

The growth curves were calculated according to the formula $L_{tn} = E\ G^n$ after Borutzky (1980) and Dussart (1969) where L_t = total length, "n" = number of copepod stage, E = egg diameter in mm, G = growth coefficient, for determination of the earlier developmental stages (egg, nauplii), which were absent from the samples.

Spatial, taxonomic, and dominance structure of planktonic communities in the southern Baltic Sea are strongly affected by prevailing abiotic and biotic conditions as well as by the degree of pollution. Autochthonous and allochthonous pollution results in increasing fertility which in turn leads to eutrophication of a water body. The species composition of the Baltic planktonic copepods, which influences the productivity of the sea, is related to climatic conditions, and affects the course of seasonal succession in the Baltic pelagic waters (Schnack, 1978, Hernroth and Ackefors, 1979; Kostrichkina, 1979, Chojnacki, 1984). Biomass assessment of Pseudocalanus elongatus in the Baltic plankton was reported by Chojnacki (1983) and Chojnacki and Hussein (1983). In this report, based on material collected in 1980 and 1981 from the Gdańsk Deep and Słupsk Trough, the individual biomass of Temora longicornis is estimated by the geometric method proposed by Chojnacki et al. (1980). The total length-weight and cephalothorax length-weight relations for an individual were determined by means of Huxley's (1932) formula:

$$W = A(L_t)B$$

where W = weight (mg), L_t= total length (mm), and A, B = equation estimators; L_c is substituted for L_t for calculation of the cephalothorax length-weight relation.

A total of 1543 individuals of all stages from copepodite I to adult was measured (Fig. 1); seasonal and regional aspects of variability in the parameters measured were taken into account.

Seasonal and spatial variabilities were found to exist in L_t, L_c, and W (Tabs. 1 and 2). Individuals of Temora longicornis attained the largest size in winter both in the Słupsk Trough and Gdańsk Deep; the smallest individuals of the species occurred in spring (Tab. 2). From Huxley's formula, W was calculated using the measured values of L_t of each copepodid stage. The equation estimators A and B and graphs obtained (Fig. 1) allow the determination of the weight of any stage, based on the mean L_t.

It is not always possible to measure egg diameter and L_t of the nauplii. However, it is possible to determine these parameters from a growth curve of the species. Assuming an almost year-round

Table 1. *Spatial variation in mean total length (L_t) and mean cephalothorax length (L_c) and mean individual weight (W) of each copepodid stage of Temora longicornis in Słupsk Trough and Gdańsk Bay. C_1 - C_5 = Copepodid stage*

Stage	Slupsk Trough			Gdansk Bay		
	L_t(mm)	L_c(mm)	W (mg)	L_t(mm)	L_c(mm)	W (mg)
C_1	0.425	0.282	0.002	0.448	0.308	0.003
C_2	0.484	0.317	0.004	0.522	0.367	0.006
C_3	0.590	0.388	0.006	0.599	0.419	0.011
C_4	0.753	0.489	0.012	0.732	0.494	0.014
C_5	0.892	0.577	0.020	0.891	0.573	0.026
male	1.281	0.776	0.047	1.029	0.666	0.036
female	1.295	0.814	0.062	1.045	0.685	0.042

Table 2. *Seasonal variation in mean total length (L_t), mean cephalothorax length (L_c) and mean individual weight (W) of each developmental stage of Temora longicornis in the Southern Baltic*

	Season											
	Autumn			Winter			Spring			Summer		
Stage	L_t	L_c	W	L_t	L_c	W	L_t	L_c	W	L_t	L_c	W
C_1	0.429	0.295	0.003	-	-	-	0.437	0.312	0.003	0.486	0.315	0.003
C_2	0.524	0.355	0.004	-	-	-	0.509	0.367	0.006	0.509	0.354	0.005
C_3	0.615	0.403	0.009	0.564	0.410	0.006	0.581	0.374	0.008	0.616	0.421	0.009
C_4	0.729	0.473	0.012	0.807	0.584	0.014	0.730	0.485	0.013	0.725	0.489	0.013
C_5	0.872	0.552	0.021	0.982	0.659	0.032	0.8885	0.576	0.021	0.882	0.570	0.023
male	1.124	0.691	0.039	1.210	0.774	0.053	1.052	0.646	0.030	1.127	0.699	0.032
female	1.098	0.702	0.045	1.252	0.790	0.061	1.092	0.691	0.041	1.126	0.714	0.049

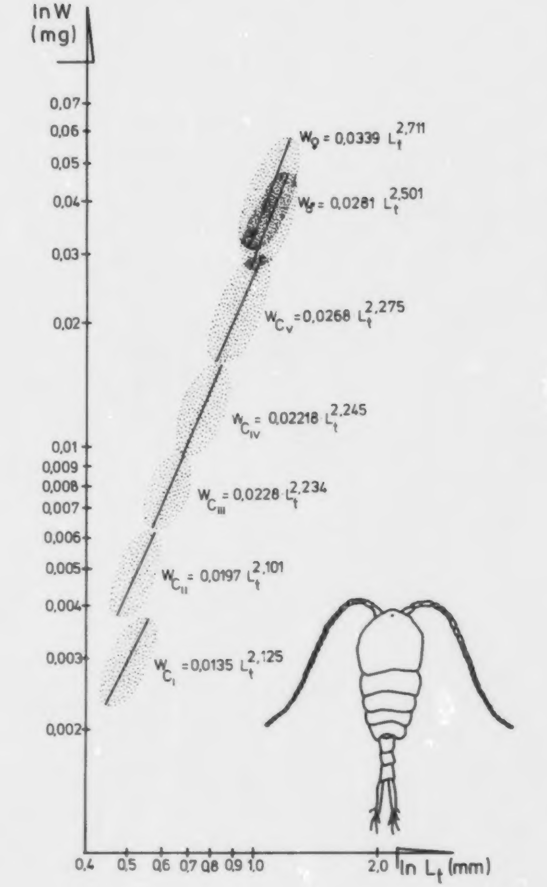

Figure 1. *Total length-weight relationship for all copepodid stages of Temora longicornis in the Gdańsk Bay.*

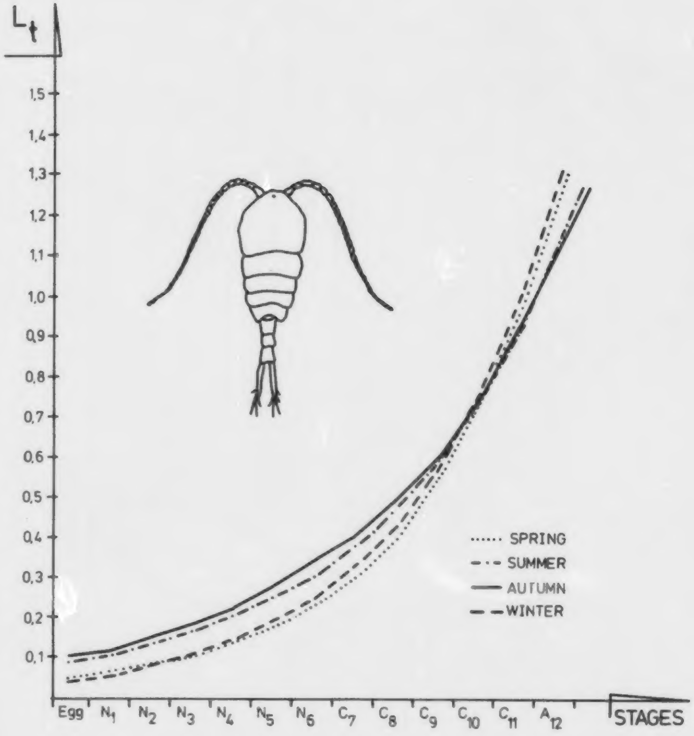

Figure 2. *Calculated seasonal means of the total length (L_t) of each developmental stage of Temora longicornis in the southern Baltic (calculated using formula of Borutzky, 1960).*

breeding, the growth rate of T. longicornis was plotted by using the formula of Borutzky (1960), successfully applied by Dussart (1969) to freswater copepods. The total length of any developmental stage and the mean growth coefficient can be calculated from these formulas:

$$L_{t_n} = EG^n, \text{ and } \quad G = \frac{L_{t_n}}{L_{t_{n-1}}}$$

where L_{t_n} = total length of n^{th} developmental stage, n = developnmental stage, starting from N_1 (first nauplius), E = egg diameter (mm), G = mean growth coefficient

The analysis of Temora longicornis growth rate shows linear dimensions of the species to be strongly correlated with abiotic environmental factors (such as water temperature, salinity etc.), the climate, and seasonality in particular (Tab. 3). The growth coefficient of the copepod attained its highest values in cold seasons and the lowest ones in warm months; the fastest growth occurred in winter and early spring (Fig. 2). Copepodites I, II, III, and V and adult individuals exhibited growth rates and mean total length independent of the season. Thus the growth rate of T. longicornis is controlled mainly by abiotic environmental factors; however, it depends also on the species physiology in terms of sexual maturation.

Table 3. *Spatial and seasonal means of total length-weight correlation, growth coefficients and estimators "A" and "B" of Huxley's (1932) Formula, for Temora longicornis.*

	Estimator		Correlation coefficient	Growth coefficient	Number of individuals
Station	A	B			
Słupsk Trough	0.0269	2.830	0.954	1.2832	428
Gdańsk Bay	0.0291	2.502	0.943	1.2834	1115
South. Baltic	0.0274	2.746	0.932	1.2833	1543
Season					
Autumn	0.0263	2.901	0.953	1.2233	615
Winter	0.0289	2.907	0.902	1.3213	173
Spring	0.0256	2.989	0.943	1.3357	222
Summer	0.0291	2.515	0.929	1.2444	533

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THE REARING OF THE MARINE CALANOID COPEPODS CALANUS FINMARCHICUS (GUNNERUS), C. GLACIALIS JASCHNOV AND C. HYPERBOREUS KROYER WITH COMMENT ON THE EQUIPROPORTIONAL RULE

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Resumé: Trois espèces du genre Calanus ont été élevées, à différentes températures et en présence d'un excès de nourriture, pour évaluer leurs vitesses de développement embryonnaire et post-embryonnaire. Les résultats supportent l'hypothèse du "développement équiproportionnel" (equiproportional development) i. e. pour toute température constante, chaque stade de développement occupe une portion similaire du temps de développement total. De plus, à partir de cette étude et d'autres études portant sur C. helgolandicus et C. pacificus, nous montrons que chez 5 espèces de Calanus, les temps relatifs nécessaires pour atteindre des stades de développement déterminés sont similaires.

INTRODUCTION

Much interest attaches to the study of development in copepods under conditions of food satiation, where physical conditions, especially temperature, operate on the physiological character of the copepod species to determine its development rates. Such development is obvious in embryonic development since food supply need not be considered.

Here we document results of laboratory rearing of embryos and larval stages of three species of North Atlantic copepods. Calanus finmarchicus and C. glacialis are basically arctic-subarctic species (Grainger, 1963) that have not been reared previously, although embryonic durations have been estimated (McLaren et al., 1969). It is remarkable that there seem to have been no laboratory rearings of young from the egg of the widespread and important C. finmarchicus other than the very limited and (as we show) evidently inadequate results reported by Marshall & Orr (1955).

Matthews (1966) captured older copepodid stages of C. finmarchicus from the Clyde Sea and kept them in natural sea water, augmented with algal food after 13 days, to estimate durations of copepodid stages CII through CV. Williams and Lindley (1980) report results of short-term experiments on shipboard to estimate intermolt durations of C. finmarchicus captured in the northern North Sea. The only complete rearings of Calanus species from egg to adult, under conditions of presumed excess of food, appear to be those by Landry (1983), who reared C. pacificus at 15°, and by Thompson (1982), who reared at several temperatures animals that she preferred not to identify to species but which we believe were C. helgolandicus (see Results and Discussion).

Throughout this study we make extensive use of the "rule" of equiproportional (Corkett, 1984) development; i.e. each developmental stage is assumed to occupy the same proportionate amount of time relative to other stages at any constant temperature. Such development was first proposed for three species of small copepods by Corkett & McLaren (1970) and here we present evidence that the species of Calanus also obey this rule.

As in past studies, we make use of Belehrádek's (1935) temperature function to describe development times (D) in days of a developmental stage or stages as a function of temperature (T) in ^{o}C by

$$D = a\,(T - \alpha)^{b}$$

where a, α and b are fitted parameters. This equation is expressed as $\log_{10} D = \log_{10} a + b \log_{10} (T - \alpha)$ and then fitted by iterating α to find a value of α giving the smallest sums of squares of deviations of observed from calculated development times, either with or without b set equal to a constant value.

The parameter b in this equation can be assigned a fixed value, for example the mean of estimated values of b obtained by fitting all three parameters to a number of species. Choosing a mean value for b for embryonic duration in an array of copepod species gives value of α that reflect differences in temperature adaptation (McLaren et al., 1969) and values of a that are correlated with egg diameter among species of Calanus (Corkett, 1972).

As in previous studies (eg. Corkett & McLaren, 1970; McLaren, 1978) our long-term aim is to develop predictive rules for copepod development, so that the tedium of laboratory rearing can be reduced. Here we show that the development times of different species of Calanus have similarities that may simplify life-history analyses and production estimates.

MATERIALS AND METHODS

Eggs used for egg and larval development were obtained from Calanus hyperboreus in February 1983 and 1984 (egg and larval development) and from C. glacialis and C. finmarchicus in early March 1984 (egg and larval development) and early June 1984 (larval development). Female C. hyperboreus were captured from the Bedford Basin, near Halifax, and the other two species from the Scotian Shelf. C. finmarchicus and C. glacialis females were separated by cephalothorax measurements. Individual females smaller than 2.6 mm were designated C. finmarchicus and individuals larger than 3.5 mm were considered to be C. glacialis. These measurements were well within the ranges of adult female cephalothorax lenghts of 2.3 - 3.4 mm for C. finmarchicus and 3.2 - 4.4 mm for C. glacialis given by Grainger (1963, his Table I). Females used for egg production were grouped in jars with 70 - 80 ml of glass-fiber filtered seawater containing a mixture of the algal flagellates Isochrysis galbana and Rhodomonas sp. and the diatom Thalassiosira weissflogii at combined cell concentrations of 3×10^{5} - 4×10^{5} cells per ml.

When eggs were used for embryonic development rates, females were examined at 2-h intervals and any eggs were placed in 10-15 ml glass-fiber filtered seawater in 25 ml vials at several temperatures. Temperatures and numbers of nauplii were recorded at 2-h intervals, allowing an estimate of the time when 50 % had hatched.

Nauplii for rearing to older stages were obtained from eggs separated from females and observed twice daily. Five to 15 nauplii were transferred to 100 ml jars containing 70 - 80 ml of glass-fiber filtered seawater (C. hyperboreus) or 65 ml glass-stoppered bottles (C. finmarchicus and C. glacialis). Glass-stoppered bottles were preferable to jars since the absence of a water-air interface avoided trapping the nauplii on the surface film. As the time for the appearance of copepodid I (CI) approached, nauplii were transferred to 100 ml jars, after which they were observed twice daily.

Animals were kept in the dark in temperature-controlled chambers in which the temperature was recorded twice a day. The cultures were exposed to light only when observations were made. The food supply was a mixture of the above-mentioned algae at a total cell concentration of 3×10^5 - 4×10^5 cells per ml. Algal cultures ca. 5 days old were used and the medium in all culture jars and bottles changed twice a week. To aid in the resuspension of food the jars were periodically swirled by hand.

We reared large numbers of animals of all three species to CI from which smaller numbers were chosen non-selectively for rearing to older stages. These chosen animals were individually placed in 100 ml jars and were maintained in the same manner as the nauplii. These jars were examined somewhat irregularly because of other commitments and the copepodid stage recorded. The rearing of *C. hyperboreus* in 1983 at ca. 3°C differed somewhat in using only *T. weissflogii* as food and in using somewhat larger jars. In the experiment conducted at ca. 8°C in June 1984 on *C. finmarchicus*, animals reaching CIII were kept individually in 200 ml jars with 170 - 180 ml of culture media. These individuals were then examined twice daily on a drained slide to determine the copepodid stage. In our analyses we use individual times to reach older stages only when these were known to within ca. 0.5 days.

The food supply for later copepodid stages was the usual algal mixture at 3×10^5 - 4×10^5 total cells per ml and the culture medium maintained and changed the same as for the nauplii. We found that *T. weissflogii* was most suitable for older stages. *Rhodomonas* sp tended to clump at higher temperatures and led to fouling and entanglement of animals, particularly young copepodids. Older copepodids experienced more difficulty in molting, often dying with the old exoskeleton still attached.

Although these rearing techniques were somewhat unrigorous, we were interested only in establishing the temperature-dependent development times under conditions of excess food supply. Individuals that showed retarded development under these conditions generally had obvious signs of damage, or were entangled in incomplete molts or in detrital masses that prevented normal swimming or feeding. Such individuals almost always died before developing further.

RESULTS

Embryonic durations

The temperature responses of embryonic development from 4 species of *Calanus* are shown in figure 1. Three species are from Nova Scotia and one from the North Sea studied by Thompson (1982). Our data for *C. finmarchicus* differ from those for this species at Tromso, Norway, presented as ranges at approximate (?) temperatures by Marshall & Orr (1953) and described by McLaren et al. (1969) using the equation $D = 1122 (T + 14.1)^{-2.05}$. Our results may be more accurate, but there is also a possibility that the Tromso animals were *C. glacialis*, which shows a similar temperature response (cf equation on Figure 1). The few data for *C. glacialis* from Nova Scotia (Fig. 1) differ from those for the same species from Frobisher Bay, N.W.T., to which McLaren et al. (1969) fitted $D = 1491 (T + 14.5)^{-2.05}$. This suggests that geographic variation may occur in this species.

We attribute data on Figure 1 from Thompson (1982) to *C. helgolandicus*, although she states that samples from her source of animals in the southern North Sea contained both *C. finmarchicus* and *C. helgolandicus*. Her results do not match our results for *C. finmarchicus*, but do resemble embryonic

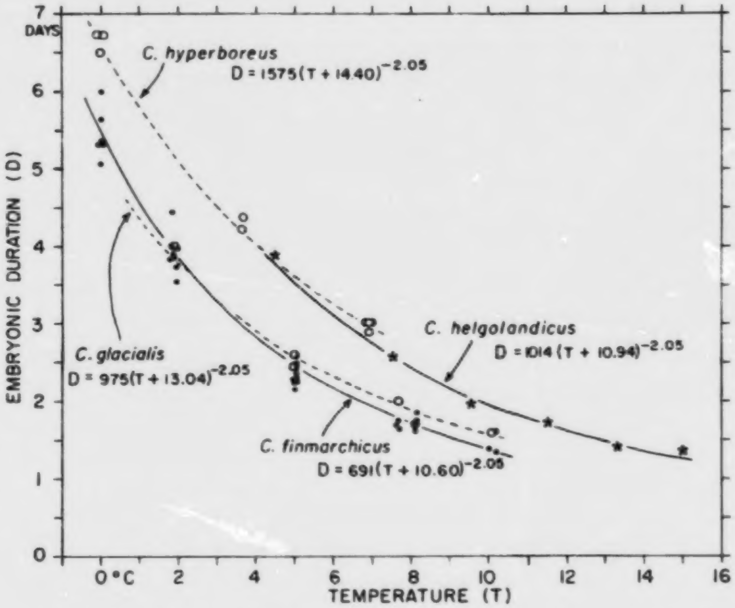

Figure 1. *Embryonic durations of 4 species of Calanus. Belehrádek's temperature functions are fitted assuming the common value of the exponent (-2.05) estimated by McLaren et al. (1969) as the mean for a number of species. Data for C. finmarchicus and C. glacialis original (see text). Data for C. hyperboreus are for Nova Scotia animals from McLaren et al. (1969, their table I). The function for C. helgolandicus is fitted to means, weighted by 1/s.e., tabulated for Calanus sp. (see text) by Thompson (1982, her Table 2).*

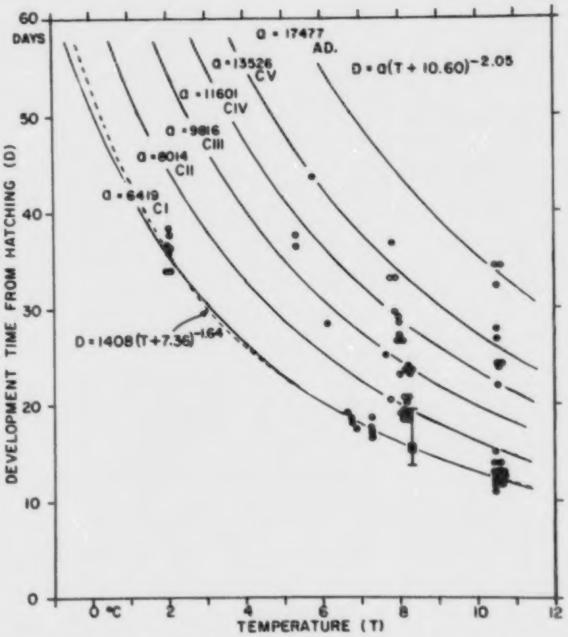

Figure 2. *Belehrádek's temperature functions for development to CI - CV and Adults of C. finmarchicus. The dashed curve for CI is the best fit for all parameters. The solid curves assume that the function for embryonic duration (fig. 1) is applicable to older stages, differing only in proportionality (a). The thick and thin bar for CI at ca. 8.3°C represent respectively 95 % c. l. of the mean and range of 70 points.*

duration of C. helgolandicus from the English Channel presented by Corkett (1972, his Table I), which can be described by the equation $D = 925\ (T + 10.26)^{-2.05}$.

Development of larval stages

Our most complete data are for C. finmarchicus which are derived from two experiments. The first was begun in March at three temperatures and the second at ca. 8.3°C in June (see Materials and Methods). As a description of times to CI, the temperature function for embryonic duration, with only a estimated (solid line Fig. 2), is practically indistinguishable from one with all parameters fitted (dashed line, Fig. 2). We are content, therefore, to fit this embryonic temperature function to the more limited data for older stages changing only the values for the parameter a (Fig. 2).

Our results for C. finmarchicus can be compared with the more limited results based on rearings of copepodid stages captured from the Clyde Sea by Matthews (1966) and from the North Sea by Williams and Lindley (1980). If stage durations implied in figure 2 apply in these eastern North Atlantic populations, then Matthew's animals were developing at near predicted rates only at younger stages (CII, CIII) at lower temperatures (0.5°, 5°), but were otherwise evidently retarded. By contrast, the instar durations estimated by Williams and Lindley (1980) were on average slightly shorter than those predicted by the equations on figure 2. However, as they tabulate intermolt times only to the nearest day or as ranges in whole days, the agreement with our results may be as good as can be expected.

Again, the data for hatching to CI of C. glacialis are adequately described by the function for embryonic development (Fig. 3). The time between CI and CIV was not adequately monitored, and the species enters a resting stage at CIV in nature on the Scotian Shelf, Nova Scotia (McLaren & Corkett, 1984) and evidently in the laboratory (our present observations), but the limited data from CIV seem to satisfy equiproportional development (Fig. 3).

We had considerable difficulty in maintaining C. hyperboreus in the laboratory, and heavy mortality and delayed development occurred among older stages. However, the curve for embryonic development again seems adequate for describing times to CI (Fig. 4). Conover (1967) found that individuals of C. hyperboreus took 57 - 75 days to reach CI at 4 - 6°C in the laboratory, and this value was used in analyses by Corkett and McLaren (1970). Clearly these animals were not developing at maximal potential rates (cf Fig. 4).

DISCUSSION

Throughout this work we have emphasised that Belehrádek's temperature function fitted to embryonic development can be used to yield curves, differing only in proportion (i. e., in a), that adequately describe times to develop to older stages of the same species. This supports the rule of equiproportional development (Corkett, in press). This rule does not depend on the use of a particular temperature function. Thus, Thompson (1982) expressed development times (D) of particular stages as functions of temperature (T) by

$$\log_e D = a - bT.$$

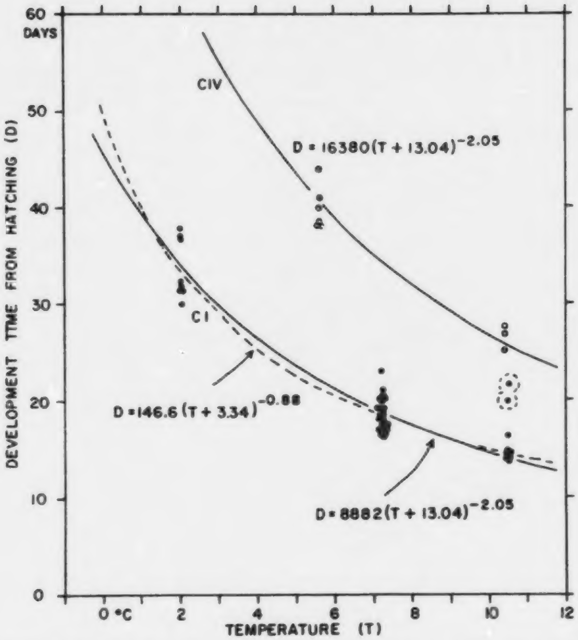

Figure 3. *Belehrádek's temperature functions for development to CI and CIV of C. glacialis. The dashed curve is the function with all parameters fitted, and the solid curves assume that the function for embryonic duration (fig. 1) is applicable to older stages, differing only in proportionality (a). Individuals within dashed circles were assumed to be abnormally delayed, and were not used in fitting curves.*

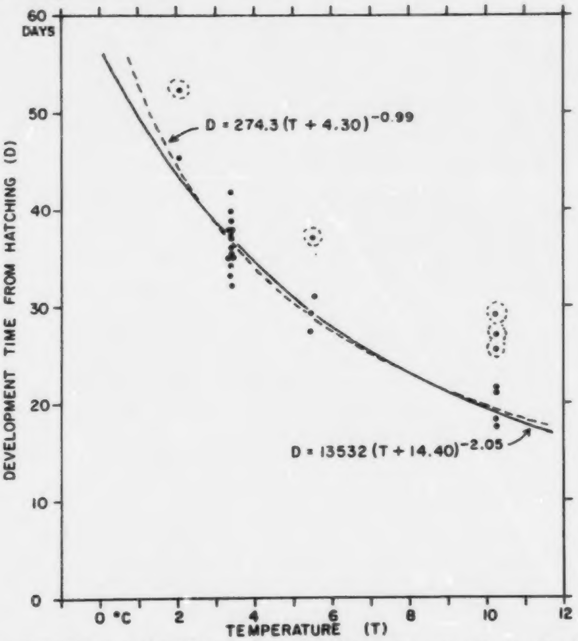

Figure. 4. *Belehrádek's temperature functions for development to CI in C. hyperboreus. The dashed curve is the function with all parameters fitted. The solid curve assumes that the function for embryonic duration (fig 1) is applicable to CI, differing only in proportionality (a). Individuals within dashed circles were assumed to be abnormally delayed, were not used in fitting the function.*

The slopes of these regressions are nearly parallel, at least after NIII (estimates of b ranging from 0.111 to 0.128). The assumptions of equiproportional development would use a common value of b to estimate a for each stage from the mean value of $\log_e D/bT$ for each individual reaching a given stage.

The assumption of equiproportional development permits greatly simplified comparisons among species (Table I). Clearly there is remarkable similarity among the five Calanus species in relative times taken to reach given stages of development. Indeed, the differences might, with more critical experiments, be seen to be largely from experimental error. Perhaps also the results for C. helgolandicus are confounded by an admixture of C. finmarchicus, although embryonic durations appear to match those for known C. helgolandicus (see Results).

Table I: *Relative times to reach various stages of Calanus spp., assuming equiproportional development. All times expressed relative to time between hatching and molting to CI.*

	Calanus species				
Developmental interval	finmarchicus[1]	glacialis[1]	helgolandicus[2]	hyperboreus[1]	pacificus[3]
egg laying to hatching	0.108	0.109	0.144	0.116	0.164
hatching to NIV	-	-	0.58	-	0.54
hatching to CI	1.0	1.0	1.0	1.0	1.0
hatching to CII	1.25	-	1.28	-	1.21
hatching to CIII	1.53	-	1.58	-	1.46
hatching to CIV	1.81	1.84	1.93	-	1.75
hatching to CV	2.11	-	2.33	-	2.15
hatching to Ad.	2.72	-	2.89	-	2.87

[1] From fig. 1 - 4.

[2] From Thompson (1982, Tables 2 and 6; mean proportions for all temperatures except 4.5° and 13.9°C, for which data are incomplete).

[3] From Landry (1983, Table 2), who gives stage durations at 15°C.

If Belehrádek's function is used to describe equiproportional development, then a can be estimated for older stages simply by dividing the estimated value for $(T - \alpha)^b$ from embryonic duration into the observed durations of the older stages at any temperature T. Alternatively, the equiproportional constants (table I) can be used to extrapolate temperature functions to older stages. Thus, Belehrádek's function for embryonic duration of C. helgolandicus (Fig. 1) can be used to estimate times from hatching to CI (assumed from table I to be 1/0.144 times the embryonic duration at any temperature) by

$$D_{CI} = \frac{1014}{0.144}(T + 10.94)^{-2.05}.$$

The estimate of a (1014/0.144 = 7042) proves to be intermediate to that for C. finmarchicus (Fig. 2) and C. glacialis (Fig. 3).

ACKNOWLEDGEMENTS

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DEVELOPMENTAL GRAZING CAPABILITIES OF PSEUDOCALANUS SP. AND ACARTIA CLAUSI (CI TO ADULT): A COMPARATIVE STUDY OF FEEDING

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Abstract: The structural morphology and functional grazing responses of Pseudocalanus sp. and Acartia clausi copepodites (CI to adult) were studied to determine the probable mechanisms employed in feeding. Over 90% of the intersetule spacings (ISS) on the second maxilla of Pseudocalanus developmental stages were ≤ 5 μm, suggesting an ability to specialize on small food particles. Only 45% (female) to 78% (CI) of the ISS on the second maxilla of Acartia copepodites were ≤ 5 um, suggesting that Pseudocalanus could theoretically specialize on smaller cells than Acartia at all developmental stages. These morphological measurements were used to calculate estimates of cell encounter, cell availability, and retention efficiency for a spectrum of phytoplankton cells. Results were presented for the youngest (CI + CII) and oldest (adult female) stages to exemplify the utility of this technique in predicting the size range of particles ingested by herbivorous copepods.

In laboratory experiments offering Isochrysis galbana and Thalassiosira weissflogii as food, Pseudocalanus developmental stages removed cells in direct proportion to their **effective** availability in the suspension. Acartia copepodites showed **apparent** (morphologically limited) selection for large Isochrysis cells. However, overall, only the adult female Acartia actively ingested cells not expected from a mechanistic model of feeding. These results were discussed in light of micro-cinematographic observations of active selection capabilities in marine herbivorous copepods.

INTRODUCTION

Many studies have indicated a close relationship between the structural morphology of the mouthparts, and the size and type of particles actually eaten by herbivorous copepods (Anraku and Omori, 1963, Marshall, 1973, Schnack, 1975, Nival and Nival, 1976, Boyd, 1976). Morphological measurements of copepod feeding appendages have been used to study the probable mechanisms involved in feeding, to estimate clearance rates and capture efficiencies for a spectrum of cells, and to predict the size and type of particles theoretically available to herbivorous copepods (Lam and Frost, 1976, Lehman 1976, Rubenstein and Koehl, 1977, Donaghay, 1980, Bartram, 1981, Dexter, 1984). However, few studies have recorded the development and growth of feeding structures of herbivorous copepods specifically to study the developmental grazing capabilities of copepods.

The paper presented at this conference reported morphological measurements from the second maxilla for the copepodite stages and adult female of Pseudocalanus sp. and Acartia clausi. These data were generated as part of a larger comparative study (Dexter, 1984) on the ontogenetic development of feeding capabilities in these two species which seasonally dominate the coastal zooplankton community off Oregon and Washington, U.S.A. The working hypothesis for the study was that there was a direct and functional relationship between the structural morphology of the second maxilla, and the spectrum of algal particles available as food to these copepods. The morphological measurements were used to calculate estimates of cell availability and capture efficiency for a spectrum of phytoplankton particles offered to copepods in laboratory grazing experiments. Results from experiments with the youngest (CI + CII) and oldest (adult female) stages were presented to exemplify the utility of this technique in predicting the size range of particles ingested by these herbivorous copepods.

METHODS AND MATERIALS

Specimen preparation: Zooplankton for this study were collected from a fjordlike embayment within Puget Sound, Washington, U.S.A., using a 64 μm mesh plankton net. The net was towed at low speed from a small boat, or hand-drawn through the surface water to collect animals. In the laboratory, six to ten individuals of each copepodite stage of *Pseudocalanus* sp. and *Acartia clausi* were sorted from preserved zooplankton samples taken during June 1979 (for *Pseudocalanus*) and July 1980 (for *Acartia*). Cephalothorax length was measured for each specimen. The feeding appendages were then removed, transferred to a clean microscopic slide, and mounted and stained with a drop of polyvinyl-lactophenol (Schnack, 1975) dyed with lignin pink (Schnack, 1982). Intersetule spacings on all setae of the second maxilla were measured by ocular micrometer (+/- 0.5 μm) at 300 and 900X using a Wild^{TR} inverted microscope.

Grazing experiments: Animals for grazing experiments were collected as described above. Collections were poured gently into insulated containers filled with surface seawater collected just prior to a tow. In the laboratory, cultures were cleaned of detritus, and maintained in large glass or plastic containers. Animals were fed a mixed suspension of *Isochrysis galbana* and *Thalassiosira weissflogii*, until several hundred copepods had been sorted for an experiment. Animals for a given experiment were then sorted by species and stage into filtered seawater containing a mixed suspension of the two experimental food types. These cultures were monitored twice daily, and maintained at a constant food level (2.5 x 10^6 μm^3/ml *Isochrysis* + 5.0 x 10^6 μm^3/ml *Thalassiosira*) during a three day preconditioning period (Donaghay 1980).

After preconditioning, healthy animals were transferred to one liter flasks containing a mixed suspension of *Isochrysis* and *Thalassiosira*. Two control flasks (phytoplankton only) and two experimental flasks (phytoplankton + copepods) were used at each of four concentration levels. Cell concentrations ranged from 1.25 x 10^6 μm^3/ml *Isochrysis* + 2.5 x 10^6 μm^3/ml *Thalassiosira* at the lowest concentration to 5.0 x 10^6 μm^3/ml *Isochrysis* + 10.0 x 10^6 μm^3/ml *Thalassiosira* at the highest concentration. On a cell volume basis, the larger cell (*Thalassiosira*, 8-15 μm equivalent spherical diameter, ESD) was twice as abundant as the smaller cell (*Isochrysis*, 2-5 μm ESD). *Isochrysis* was therefore ten times as abundant as *Thalassiosira* on a cell number basis. These concentrations were chosen to represent the full range of ***in situ*** concentrations that nearshore copepods generally encountered in the field, yet were within the range of concentrations reliably counted on an electronic particle counter. Initial and final (24 hour) cell counts were taken using a model ZB_i Coulter^{TR} particle counter interfaced to a 64 channel analyser, oscilloscope, and plotter. Rate calculations were made using typical equations (Frost 1972) modified for phytoplankton growth over the 24 hour experimental period (Donaghay 1980, Dexter 1984). The size-class-specific grazing calculations were grouped into size categories which represented cell size intervals of 1 um ESD in order to relate the grazing data to the morphological measurements directly. Values for R_i = the % contribution to the ration from a cell size category, *i*, and P_i = % total cells available for ingestion from that size class, were calculated for the 1 μm size categories (i = 2-15 μm ESD). These experimental procedures are described in detail elsewhere (Donaghay, 1980, Dexter, 1984).

RESULTS

The R_i (observed ration) values were statistically compared to the P_i (expected ration) values generated from experiments conducted with each developmental stage of Pseudocalanus and Acartia. These proportions were calculated using the equations:

$$\textbf{Encounter Rate } (C_i) = F_{max} \cdot N_i \, , \qquad (1)$$

where F_{max} = maximum filtration rate, and N_i = exponential mean number of cells in size category **i**;

$$\textbf{Retention Rate } (R_i) = C_i \cdot E_i \, , \qquad (2)$$

where C_i = encounter rate as calculated in equation (1), and E_i = the theoretical retention efficiency for a cell in size category **i**; and

$$\textbf{Effective Cell Availability } (A_i) = N_i \cdot E_i \, , \qquad (3)$$

The E_i values (equations 2 and 3) were calculated from the relative abundance of intersetule spacings measured on the second maxilla for each developmental stage of Pseudocalanus and Acartia. These pore size were grouped into effective pore size categories (1 µm intervals), assuming that an overlap of 1 µm was necessary between the measured pore size and the diameter of a cell, for effective retention of the particle by the appendage. The relative percent frequency for each effective pore size category was defined as the theoretical retention efficiency (E_i) for that particle size. These data were generated for each developmental stage (mean of 4 to 6 specimen), and used to analyze results from the laboratory grazing experiments.

The R_i and P_i proportions calculated for the youngest (CI + CII) and oldest (female) stage exemplified the responses typically obeserved in grazing experiments with Pseudocalauns. For Pseudocalanus, there were no significant differences ($p < 0.05$, chi-square analysis) between the observed (R_i) and expected (P_i) proportions of cells eaten over the complete cell distribution (2-15 µm ESD). In contrast, Acartia females tested at the same food levels preferently removed large cells within the Isochrysis distribution and small cells from the Thalassiosira distribution ($p < 0.05$). Acartia copepodites also showed an apparent preference for larger cells within the Isochrysis distribution, resulting in proportions which, overall, were significantly different from the expected proportions of cells available to these grazers across the two-food distribution. However, analysis with proportions caculated from each cell type distribution individually (i.e., tests running on 2-5 µm = Isochrysis cells compared to test run on 8-15 µm = Thalassiosira cells), analysis of the cell number and cell volume data directly (Kolmogorov-Smirnov statistic), and analysis of selection patterns (relativized electivity index, Vanderploeg and Scavia, 1979), all supported the hypothesis that the developmental stages of Pseudocalanus (CI to adult) and the younger stages of Acartia removed cells in direct proportion to their **effective** availability within the particle spectrum. The Acartia female was the only developmental stage tested that actively altered its selection of particles away from that expected, based on a mechanistic "filtration" model of feeding.

DISCUSSION

Even though food particles are not actively "sieved" from the water by the beating of the feeding appendages of "filter-feeding" copepods, particles are, nevertheless, sensed and retained by these appendages during the normal feeding process of herbivorous, suspension-feeding copepods (Koehl and Strickler, 1981, Strickler, this issue). Small intersetule spacings, generally found at the bases of setae (Marshall, 1973, Dexter, 1984), preclude the flow of water through a pore due to the entrainment of water around the moving appendages, and the subsequent formation of a relatively thick boundary layer. Closely-spaced setules therefore result in setae that are functionally smooth (Koehl and Strickler, 1981), which may be used to capture and manipulate parcels of water for the effective removal of small particles (Boxshall, this issue, Strickler, this issue). Widely-spaced setules, generally found toward the tips of setae (Marshall, 1973, Dexter, 1984), may allow some water to pass through a pore due to the reduction in size of the boundary layer around a faster-moving object (Boxshall, this issue, Strickler, this issue), but still results in the efficient capture of both large, non-motile and mobile food items. The overall pattern of setule spacings across the appendage may thus determine the pattern of water flow around the feeding appendages, and affect what size or types of particles bump into, or are manipulated toward the feeding appendages (Koehl and Strickler, 1981).

A prerequisite for specialization on small food particles is therefore the evolution of appendages with a high percentage of small intersetule spacings. This adaptation was exemplified by the feeding morphology of Pseudocalanus developmental stages, which had greater than 90% of the intersetule spacings on the second maxilla ≤ 5 µm. The larger intersetule spacings found on all developmental stages of Acartia clausi (45-78% of the intersetule spacings were ≤ 5 µm) suggested an adaptation for specializing on larger, and possibly motile food items, and resulted in their apparent (i.e., morphologically-limited) selection for large particles within the Isochrysis distribution.

Such morphological adaptations for particle selection certainly interact with chemosensory, physiological, and perhaps behavioral capabilities, to produce a variety of feeding responses which allow planktonic "grazers" to cope with the rapidly changing food spectra present in estuarine and coastal marine environments (Sheldon et al., 1972). With careful analysis of data generated in traditional laboratory grazing experiments, coupled with the extension of microcinematographic observations to coastal zooplankton species, it would appear that a general paradigm is developing to explain the evolution of both "active" and so-called "passive" responses of suspension-feeding marine copepods. Marine copepods do behave in the sense that they respond to physical and biological variables in their environment in more than just a passive manner, and thus remain attuned to the vagaries of a planktonic existence. However, different adaptations may have evolved in response to physical and biological events which copepods from different environments experience at varying spatiotemporal frequencies (Dexter, 1984).

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CHANGES IN THE SPECIES COMPOSITION OF HARPACTICOIDA (COPEPODA) IN VISTULA LAGOON, PUCK BAY, AND SOUTHERN BALTIC

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Abstract: Figures and tables of the poster presented show changes which occurred in the composition of harpacticoid copepod communities between 1930 and 1962 in the Puck Bay and between 1965 and 1981 in the southern Baltic. Knowledge of the basic environmental factors operating in the area during the periods studied makes it possible to trace ecological causes of disappearance of some harpacticoid species and appearance of others in the regions under study. The 1962, 1965 and 1981 data were worked out by the present author, while the 1930 results were reported by Jakubisiak.

INTRODUCTION

Changes which occurred in species composition and distribution of harpacticoid copepods in the Vistula Lagoon, Puck Bay, and southern Baltic waters adjacent to the Polish coast are presented. Data collected by the present author and others are dealing with harpacticoids of the area are used.

RESULTS AND DISCUSSION

The results obtained are presented in Table 1 and Figure 1. A number of species (Nos. 1, 8, 9, 14, 24, 26, 33, 37, 38, 39, and 42 in Tab. 1) occur in the southern Baltic and in either or both Vistula Lagoon and Puck Bay.

Some species were found in only one of the three regions: Nitocra hibernica in Vistula Lagoon; Phyllognathopus viguieri, Schizopera clandestina, S. compacta, Nitocra typica, N. lacustris, and Mesochra aestuarii in the Puck Bay; and Halectinosoma finmarchicum, Pseudobradya sp., Microsetella norvegica, Arenosetella germanica, Danielssenia typica, Tisbe furcata, Dactylopodia euryhalina, Tachidiella minuta, Stenhelia gibba, Robertgurneya spinulosa, Amphiascoides debilis, A. dispar, Ameira parvula, Schizopera baltica, S. ornata, Nitocra fallaciosa f. baltica, Pseudameira reducta, Scottopsyllus minor, S. herdmani, Stenocaris minuta, Heteropsyllus major, and Laophonte baltica in the southern Baltic. Some species (Nos. 4, 6, 7, 12, 27, 34 in Tab. 1) were found in their respective area only once.

Several harpacticoid species found off the Polish coast are new to the Baltic proper. Eight such species, Halectinosoma finmarchicum, Tachidiella minuta, Stenhelia gibba, Robertgurneya spinulosa, Amphiascoides debilis, A. dispar, Ameira parvula, and Pseudameira reducta, along with a species of the genus Pseudobradya, probably new to science, were found in 1981. Six out of the eight species new to the Baltic proper (Tachidiella minuta, Stenhelia gibba, Robertgurneya spinulosa, Amphiascoides debilis, A. dispar, and Pseudameira reducta) occur exclusively at greater depth (ca. 80 m), beneath a stream of

Table 1

Area	Vistula Lagoon			Puck Bay					Southern Baltic		
Year of collection	1911?	1917?	1962	1928/ 1929	?	1962	1964	1981?	1965	1981?	1981
Reference	Vanhöffen 1911	Vanhöffen 1917	Drzycimski et Różańska 1967	Jakubisiak[1] 1930	Minkiewicz (Demel, 1936)[2]	Drzycimski 1967	Sywula 1966	Sywula 1982	Drzycimski 1974	Sywula 1982	Drzycimski unpublished
Species											
1. Halectinosoma curticorne (Boeck)			O		O	O	O		O	O	O
2. Halectinosoma finmarchicum (T. Scott)											⦶
3. **Pseudobradya sp.**[3]											⊙
4. Microsetella norvegica (Boeck)									θ[4]		
5. Arenosetella germanica Kunz										⊗	⊗
6. Phyllognathopus viguieri (Maupas)					θ						
7. Leptocaris brevicornis (van Douwe)		θ		θ							
8. Tachidius discipes Giesbrecht		O	O	O		O	O		O	O	O
9. Microarthridion littorale (Poppe)			O	O		O	O		O		O
10. Danielssenia typica Boeck									⊗		⊗
11. Tisbe furcata (Baird)									⊗		⊗
12. Dactylopodia euryhalina[7] (Monard)									θ[5]		
13. Tachidiella minuta Sars											⦶
14. Stenhelia palustris Brady[7]					O	O			O		O
15. Stenhelia gibba Boeck											⦶
16. Robertgurneya spinulosa[7] (Sars)[7]											⦶[6]
17. Amphiascoides debilis (Giesbrecht)											⦶[6]
18. Amphiascoides dispar[7] (T. & A. Scott)											⦶
19. Schizopera clandestina (Klie)						⊗		⊗			
20. Schizopera compacta De Lint								O			
21. **Schizopera baltica** Lang									⊗		⊗
22. **Schizopera ornata** Noodt et Purasjoki									⊗		⊗
23. Ameira parvula (Claus)											⦶
24. Proameira hiddensoensis (Schäfer)						O			O		O
25. Nitocra typica Boeck					⊗	⊗	⊗	⊗			
26. Nitocra spinipes Boeck		O		O		O	O	O	O		O
27. Nitocra fallaciosa f. baltica Lang									θ		
28. Nitocra lacustris Schmankevitsch						⊗	⊗				
29. Nitocra hibernica (Brady)[7]	⊗	⊗									
30. Pseudameira reducta Klie											⦶
31. Scottopsyllus minor (T. & A. Scott)									⊗		⊗
32. Scottopsyllus herdmani (T. & A. Scott)									⊗		⊗
33. Remanea arenicola Klie					O	O			O	O	O
34. Mesochra rapiens (Schmeil)		θ		⊗		⊗	⊗				
35. Mesochra aestuarii Gurney					⊗		⊗				
36. Stenocaris minuta Nicholls									⊗		⊗
37. Paraleptastacus spinicauda (T. & A. Scott)				O	O	O O			O O	O	O O
38. Nannopus palustris Brady						O			O		O
39. Huntemannia jadensis Poppe			O	O		O			O		O
40. Heteropsyllus major (Sars)									⊗		⊗
41. Laophonte baltica Klie									⊗		⊗
42. Paronychocamptus nanus (Sars)				O		O	O		O		
43. Onychocamptus mohammed (Blanchard et Richard)		θ		⊗		⊗	⊗				

Table 1 (continued)

O species known from the Southern Baltic and found also in one or both remaining areas
⊗ species present in the area studied in at least two periods of study
⊖ species found only once in the area

⦶ species new for the Baltic proper
⊙ species new for science

names of species known exclusively from the baltic are in bold

1 = Demel (1933) refers to data already published by Jakubisiak (1930)
2 = Demel (1936) refers to unpublished Minkiewicz's data
3 = Drzycimski (1974) has wrongly identified them as *Halectinosoma abrau* and *Halectinosoma elongatus*.
4 = found in a plankton sample
5 = found by Monchenko (1967)
6 = data published by Drzycimski (1983)
7 = species found exclusively at large depths underneath the North Sea waters.

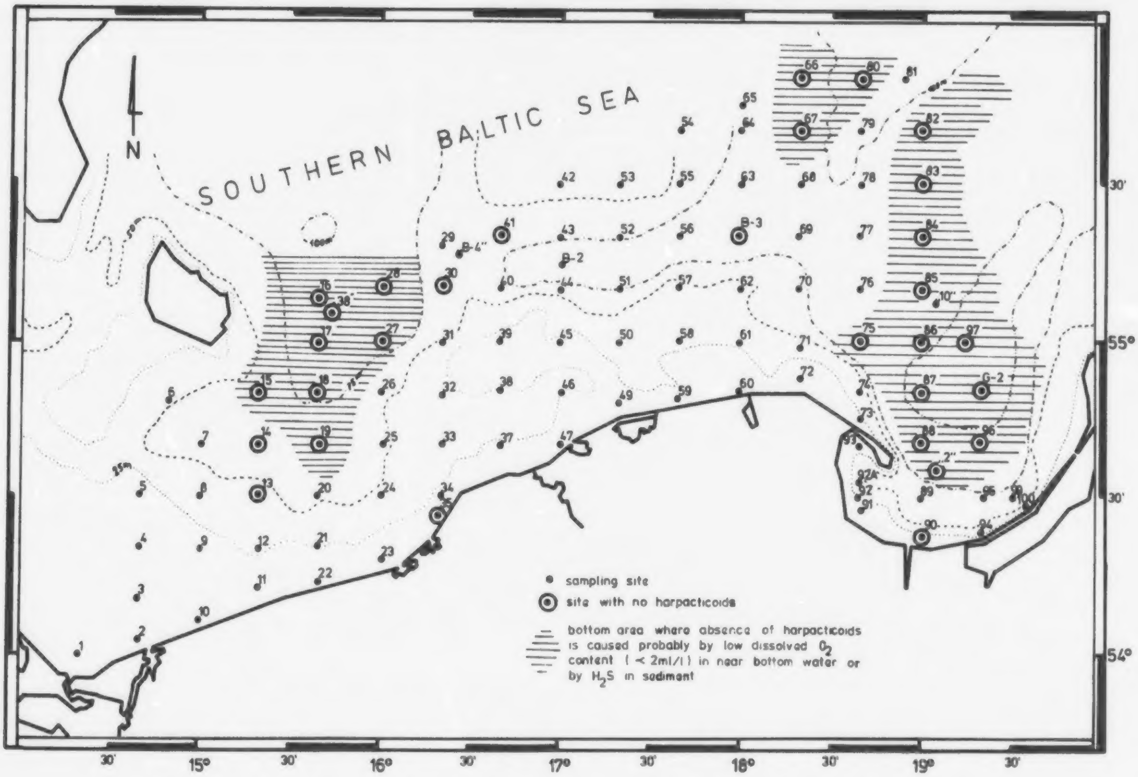
SOUTHERN BALTIC SEA
N
100m
25m
sampling site
site with no harpacticoids
bottom area where absence of harpacticoids is caused probably by low dissolved O_2 content (< 2ml/l) in near bottom water or by H_2S in sediment
B-2
B-3
B-4
G-2
30'
55°
30'
54°
30'
15°
30'
16°
30'
17°
30'
18°
30'
19°
30'

Figure 1: *Sampling stations of the present study in the southern Baltic Sea.*

water flowing in from the North Sea (Fig. 1). The salinity of this water exceeds 10 ‰.

Figure 1 also shows three deep areas where the bottom water has low oxygen content (less than 2ml/l) and the sediment contains hydrogen sulphide. No harpacticoid copepods were found from these areas in 1981. Samples collected from the same areas in 1965 (except from the Gotland Deep, not covered by that study) contained such species as Halectinosoma curticorne, Proameira hiddensoensis, Paraleptastacus spinicauda, and Huntemannia jadensis (Drzycimski, 1974).

It is therefore apparent that environmental conditions unfavourable for the harpacticoids have been spreading to a larger area of the southern Baltic benthic ecosystem.

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E. DADAY: HIS WORK ON COPEPODA AND EXTANT MATERIAL

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Abstract: E. Daddy (1855-1929) worked on the systematics of nearly all groups of aquatic microfauna during his scientific career of over 40 years. He published on over 100 scientific topics and altogether 225 papers and books mark his achievements. About half of his work are studies on Crustacea, his contributions to the knowledge of microcrustaceans being of great significance.

The extant material of the **Collectio Dadayana** is mainly composed of these animals. His Crustacea collection consists of 1900 tubes of alcoholic specimens and 1800 microscopic preparations. The copepod material consists of 282 tubes and 480 slides, representing 157 copepod species as identified by Daday himself. Of the 75 taxa desrcibed by Daday, 60 have original specimens in the collection, which may hopefully be put to use in solving current problems in copepodology.

Eugene Daday (Fig. 1-3) descendant of one of the oldest families of intellctuals in Hungary, was born in 1855. He received his primary schooling as well as his secondary school education at Kolozsvár, where he was graduated from the gymnasium in 1874. In the same year he enrolled in a course in natural history and education at the University of Kolozsvár, he received his Ph. D. in natural history in 1878. He worked at the Department of Zoology and Comparative Anatomy, University of Kolozsvár until 1885 and gave a course entitled "Invertebrates of inland waters". He spent the period from September 1885 to May 1886 on a scholarship at the Stazione Zoologica of Naples. After his return he applied for a curatorship at the Zoological Department of the National Museum, Budapest. He filled this post for 15 years. In 1902 he was offered the chair of Zoology at the Budapest Institute of Technology, where he worked up to 1920. In the spring of 1920 he fell ill, contracted bronchitis and his condition was worsened by asthma from which he had suffered ever since his early youth. He died on the 2nd of April, 1920.

Dady worked with unparalleled diligence; he worked long hours and with great speed. He studied the systematics of nearly all groups of the freshwater microfauna. His scientific work of over 40 years was published on about 7000 printed pages. He discovered the following taxa new to science: 3 suborders, 8 families, 12 subfamilies, 42 genera, 9 subgenera, 801 species and 103 varieties. He was asked to study materials of several museums in Europe and he was commissioned to report on material collected by several renowned expeditions of his time. It is through his studies that new data were obtained on the microfauna of the up to then little-known parts of the world, such as the Antarctic, Paraguay, Chile, Ceylon, India, Tibet, New Guinea, Asia, German East Africa.

Over half of Daday's scientific works deal with Crustacea. He was the first specialist in the National Museum to work on Crustacea and he was responsible for setting up a collection, primarily made up of microcrustaceans. Daday was greatly interested in "Entomostraca" ever since his early days in Kolozsvár. He made several collecting trips in Transylvania and published a catalogue of Crustacea of this country in 1884. Later, while on the staff of the museum, he led field expeditions to most parts of Hungary. The results were published in several faunistic papers, but on the basis of his material he monographed the Hungarian species of Branchipus, the Cladocera, Copepoda, and Ostracoda. He

Figure 2. *Daday in his study*

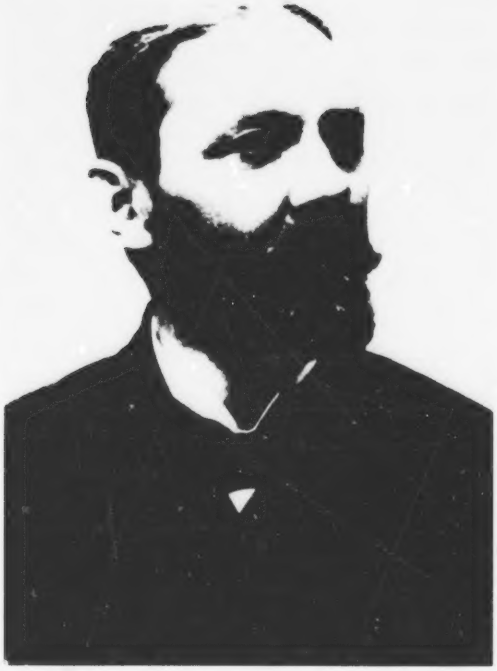

Figure 1. *Eugen Daday 1855 - 1920*

Figure 3. *Daday with his wife and son.*

elaborated chapters on crustaceans in the series Fauna Regni Hungariae and the Balaton monograph. Daday's many-sided research activity in Hungary gained him international reputation. He reported on material collected by Hungarian collectors, plankton samples were collected for him by L. Biró in New Guinea, by L. Almási in Asia, and E. Ciski collected for him on the Eugene Zichy expedition in Russia and Siberia. Several foreign collectors also sent materials to Daday for study (from Paraguay, Patagonia, Mongolia, Africa, etc.). His enormous, comprehensive studies on the plankton of these areas are fundamental works for the study of the microfauna of the inland waters for these regions. Annandale, of the Calcutta Museum sent him a rich material from the East Indies, which was actually Daday's last large project. He finished his manuscript in 1918, but this work was never published and the manuscript is now lost.

Daday published 43 papers, in which he described new copepod species or referred to species described by him. About half of these papers concern the Hungarian copepod fauna, while the remaining ones deal with copepods from various parts of the world (Ceylon, New Guinea, Patagonia, Chile, Turkestan, Paraguay, Sumatra, Mongolia, German East Africa, Tibet). Almost all papers were published in two versions, that is in Hungarian and in an other language (German or Latin). With the exception of a few papers these versions are not equivalent ones (they were published in different years and/or in different journals). These circumstances must be taken into consideration in any critical decision concerning date of publication. It is worth mentioning that Daday published his papers with various author names corresponding with the language of the publications. Hungarian papers with Daday Jenó, German papers with Eugen von Daday and papers in Latin with the name Eugéne Daday de Dées. All of these names are that of Daday, of one person. His taxa should be referred simply to Daday. According to a list made by Daday himself, he described 78 new copepod taxa (3 genera, 73 species and 2 varieties).

Daday set up a collection and a valuable library, his collection was purchased by the Natural History Museum in 1927 and is now deposited in the Crustacea Collection of the Zoological Department. The extant material of the Collectio Dadayana is mainly composed of microcrustaceans. It consists of 1850 tubes of alcoholic specimens and 1800 microscopic preparations. The copepod material consists of 282 tubes and 480 slides, representing 157 copepod species as identified by Daday himself (Table I). Of the 78 taxa described by Daday, 60 have original specimens in the collection. Unfortunately, type designations were made by Daday only in few cases (labelled simply as "Typus") thus it would be highly desirable - when studying this material - to select lectotypes and paralectotypes. In addition to material of taxa, specimens of other species also are kept in the collection, including unpublished material from India (e.g. there are fifty tubes labelled "Mesocyclops leuckarti"). Nothing is known about the material which Daday used for embedding the specimens on slides. It is regrettable that many slides have dried out but some of them are worth remounting.

Table 1. *List of Copepoda of the Collectio Dadayana, deposited in the Hungarian Natural History Museum, Budapest (t = alcoholic specimens in tubes, s = mounted specimens on slides) (Species names are given following the original labelling by Daday).*

HARPACTICOIDA

Attheyella decorata	-, s	Ectinosoma australe	-, s
Attheyella grandidieri	-, s	E. barroisi	t, -
		E. edwardsi	-, s
Canthocamptus bidens	t, s		
C. brevicornis	-, s	Laophonte chathamensis	t, s
C. crassus	- s	L. mohammed	t, s
C. dentatus	- s		
C. incertus	-, s	Maraenobiotus affinis	t. -
C. insignipes	-, s		
C. longirostris	-, s	Mesochra blanchardi	t, -
C. longisetosus	-, s	M. brevicornis	t, s
C. minutus	-, s	M. deitersi	t, s
C. northumbricus	t, s	M. meridionalis	t, s
C. ornatus	-, s		
C. papuanus	-, s	Nitocra brevisetosa	-, s
C. signatus	t, s	N. fragilis	t, s
C. staphylinus	-, s	N. paradoxa	t, s
C. treforti	-, s	N. platypus	t, -
C. trispinosus	-, s		
		Onychocamptus curvipes	t, s
		O. mongolicus	-, s

CYCLOPOIDA

Cyclops aequorus	-, s	Cyclops elongatus	-, s
C. affinis	-, s	C. entzii	-, s
C. agilis	t, s	C. fimbriatus	t, s
C. albidus	-, s	C. frivaldszkyi	-, s
C. anceps	t, s	C. fuscus	t, s
C. annulatus	-, s	C. gracilis	t, s
C. aspericornis	-, s	C. horváthi	-, s
C. attenuatus	t, s	C. hungaricus	-, s
C. bathybius	-, s	C. indicus	-, s
Cyclops bicolor	t, s	C. irritans	-, s
C. bicuspidatus	t, s	C. languidus	-, s
C. brevisetosus	-, s	C. leuckarti	t, s
C. chilensis	t, -	C. lucidulus	-, s
C. ciliatus	-, s	C. macrurus	t, s
C. claudiopolitanus	-, s	C. margói	-, s
C. diaphanus	-, s	C. nivalis	-, s
C. dybowskii	t, s	C. oithonoides	t, s

Table I (continued)

CYCLOPOIDA

Cyclops ornatus	-, s	*C. spinifer*	t, s
C. paradyi	-, s	*C. strenuus*	t, s
C. fimbriatus	-, s	*C. tenuicornis*	-, s
C. frivaldszkyi	t, s	*C. tenuicaudis*	-, s
C. fuscus	t, s	*C. varicans*	t, s
C. gracilis	-, s	*C. vernalis*	t, s
C. horváthi	-, s	*C. vicinus*	t, s
C. hungaricus	t, s	*C. vietsi*	-, s
C. indicus	-, s	*C. viridis*	t, s

CALANOIDA

Acartia dubia	t, -	*Diaptomus galebi*	-, s
A. latisetosa	t, s	*D. gracilis*	-, s
		D. kraepelini	t, s
Boeckella brasiliensis	-, s	*D. kilimensis*	t, s
B. dubia	t, s	*D. laciniatus*	t, s
B. entzii	t, s	*D. lobatus*	-, s
B. longicauda	t, s	*D. lobifer*	-, s
B. setosa	t, -	*D. lumholtzi*	t, s
B. sylvestryi	t, s	*D. orientalis*	t, s
		D. parvulus	-, s
Diaptomus acutilobatus	-, s	*D. paulseni*	t, s
D. aethiopicus	-, s	*D. pulcher*	t, s
D. affinis	-, s	*D. salinus*	t, s
D. africanus	t, s	*D. semicingulatus*	-, s
D. alluaudi	-, s	*D. similis*	t, s
D. amblyodon	t, s	*D. singalensis*	-, s
D. anisitsi	-, s	*D. spinosus*	t, s
D. asiaticus	-, s	*D. strigilipes*	t, s
D. bacillifer	t, s	*D. stuhlmanni*	t, s
D. blanci	t, s	*D. tatricus*	t; -
D. bangaloricus	-, s	*D. theeli*	t, s
D. bouvieri	t, s	*D. tibetanus*	t, s
D. castor	t, s	*D. transitans*	-, s
D. chaffaryoni	t, s	*D. vicinus*	-, s
D. cinctus	t, s	*D. viduus*	-, s
D. coeruleus	t, s	*D. visnu*	-, s
D. conifer	t, s	*D. wierzejskii*	t, s
D. consors	-, s	*D. zachariasi*	-, s
D. contortus	t, s	*D. zichy*	-, s
D. doriai	t, -		
D. elegans	t, s	*Eurytemora lacinulata*	-, s

Table 1 (continued)

CALANOIDA

Hemidiaptomus ignatovi	t, -	*Pseudoboeckella bergi*	t, -
		P. gracilis	t, s
Heterocope saliens	t, -	*P. gracilipes*	t, s
		P. pygmea	t, s
Limnocalanus sarsi	t, s		
		Pseudodiaptomus ernesti	t, s
Lovenula greeni	t, -	*P. lobipes*	t, s
		P. serratus	-, s

A more detailed catalogue about Daday's work on Copepoda and his copepod collection is under preparation and will be published. It contains a list of his papers on Copepoda, a list of the copepod species described by him, indicating the present status of each taxon and a list of all copepod material. It is also hoped that this short paper will provide an incentive for specialists in Copepoda to study Daday's material.

ACKNOWLEDGEMENTS

I am deeply indebted to Dr. C.-t. Shih and Dr. G. Schriever for their support, which made the presentation of this paper possible.

COPEPOD GRAZING ON A RED TIDE DINOFLAGELLATE

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Abstract: This presentation describes a reasearch project that is designed to characterize the relationship between copepod ingestion rates and the cell toxin levels in clonal isolate cultures of a red tide dinoflagellate. This work is still in progress, and no definitive grazing results are yet available. Outlines are given of the study's conceptual background and pratical methodology.

BASIC CONCEPT OF EXPERIMENTS

Three clones of the red tide dinoflagellate *Gonyaulax tamarensis* are involved in the study. The first, Ply173, is non-toxic and weakly luminescent. The second, GT429, is strongly toxic and luminescent. The third, Wh#7, which has just been acquired, is reported to be extremely toxic. It is presumed to be luminescent as well, although measurements have not yet been made to verify this. These clones are represented in unm[illegible] cultures to adult females of the neritic copepod species *Pseudocalanus* sp. and *Acartia hudsonica* [illegible] separate sessions.

The question of whether *Gonyaulax* cell toxin levels influence copepod grazing has not been adressed specifically in previous works. It has been shown, however, that dinoflagellate luminescence has a negative effect on grazing (Esaias and Curl, 1972, White H., 1979). With the *Gonyaulax* clones available, it is not possible to vary toxicity independently of luminescence, but it is possible to vary luminescence independently of toxicity. This permits the quantification of the influence that luminescence has on copepod grazing. By substracting this factor from the grazing response to the combined influence of luminescence and toxicity, the influence of toxicity alone on copepod grazing can be isolated.

Background - Red Tide Blooms. *Gonyaulax tamarensis* is the organism reponsible for outbreaks of paralytic shellfish poisoning in coastal regions of eastern Canada and the New England states. Blooms occasionally reach red tide proportions, essentially unialgal patches at or near the surface, with concentrations of millions of cells per litre. The dynamics of these blooms are governed by the combined actions of intrinsic factors (e.g. life cycle characteristics, motility, copper sensitivity) and extrinsic factors (e.g. physical, chemical, and biological environmental conditions).

Steidinger (1983) has described a generalized pattern of dinoflagellate bloom dynamics which involves four stages: initiation, growth, accumulation, and dispersal. Initiation is the stage during which the water column is seeded with motile cells by excystment of the overwintering benthic hypnozygotes, responding to environmental (and perhaps also endogenous) cues. Growth is the stage during which this seed population increases in numbers to achieve moderate background concentrations over an extended area. The third stage, accumulation, decribes the onset of the bloom proper and is accomplished by physical advective processes combing with behavioural movements to concentrate dinoflagellates in dense surface patches. The fourth stage, dispersal, occurs when the physical concentrating mechanisms cease or reverse their action. The dominance of physical factors in the latter stages of the bloom is also suggested by two additional bits of evidence: dinoflagellate growth rates are too low to solely account for bloom development, and conditions for dinoflagellate growth remain suitable for dinoflagellate growth even after the dispersal of bloom patches.

The role of zooplankton grazing pressure in influencing bloom dynamics has been investigated for Gonyaulax tamarensis to some extent in the field (White A., 1979, Turner and Anderson, 1983) and in the laboratory (White H., 1979, White A., 1981). Much remains to be investigated about this single element of a complex system. The laboratory study described here addresses the specific question of whether the toxins produced by the dinoflagellate have any effect on the grazing behaviour of two important members of the zooplankton assemblage, Pseudocalanus sp. and Acartia hudsonica.

STUDY ORGANISMS

1. The dinoflagellate

Gonyaulax tamarensis has a life cycle that alternates between a benthic diploid hypnozygotic cyst, the overwintering phase, and a planktonic haploid motile cell, the phase manifested in red tide blooms. The motile cell is the phase encountered by copepod grazers. It is a roughly spherical cell, ranging in diameter from 25-40 μm, and has a cell wall of cellulosic plates. In terms of biochemical composition, Gonyaulax tamarensis has several times the amounts of protein, lipid, and carbohydrate possessed by a typical diatom of equivalent volume (Hitchcock, 1982). This consideration, combined with the size and (seasonal) availability of this species, suggests that it should be a highly acceptable food source to copepods which occur in the regions and seasons of Gonyaulax blooms.

2. The copepods

Pseudocalanus sp. and Acartia hudsonica are small calanoid copepods of about 900-1200 μm length. Their field distributions overlap to some extent, although Pseudocalanus sp. tends to occur in deeper, more off-shore waters while A. hudsonica tends to occur in shallower, more near-shore and estuarine waters. Both coincide in region and season with Gonyaulax blooms. Both are omnivorous, with Pseudocalanus sp. using a smooth cruising mode of foraging and A. hudsonica a more erratic, darting style. This difference in foraging behaviour is one of the reasons that these two species were chosen for the present study. H. White (1979) demonstrated that Acartia sp. provokes much more luminescent flashing than Pseudocalanus sp., and the grazing rates of the two species on Gonyaulax cells may reflect this difference.

Another reason for the choice of these two copepod species is their relative accessibility for the laboratory experiments throughout the year. Collections are made using small craft and hand-drawn nets in the North West Arm and Bedfort Basin, two embayments adjacent to the city of Halifax, Nova Scotia.

Experimental Design

The basic experiment in this research project is a grazing session of ten hours duration, in which four grazing bottles and two controls at each of four cell concentrations are run, using one copepod species and one dinoflagellate clone per session. Before and after counts of cell concentrations are made on each bottle using a Coulter Counter Modell TAII. Subsamples for toxin extraction are taken from pooled cultures both before and after the session. Luminescence levels are monitored throughout the session using an ATP photometer.

From 10-15 adult female copepods are used in each 250 ml grazing bottle, and they are preconditioned before each session at moderate concentrations of the non-toxic Ply173 culture. Each session is run within the scotophase of the dinoflagellate's luminescence cycle; partly to avoid complications with the shifting of luminescence capacity from high to low levels, and partly to avoid discrepancies in cell counts brought about by phased cell divisions, which typically occur just after the onset of the photophase.

At least four grazing sessions are required for each copepod species; one with each of the three clones, and a fourth with a split culture in scotophase halves to obtain a correction factor for the influence of luminescence on grazing.

Copepods are counted and inspected both before and after each session, and fecal pellets are counted in subsamples drawn off and preserved after each session. Ingestion rates are determined with a data analysis computer program devised by C.M. Boyd utilizing the equations of Frost (1972).

Toxicity

Endogenous neurotoxin production is a species characteristic of *Gonyaulax tamarensis*, with wide variations among populations in different regions, and in the proportions and absolute amounts of the molecular variants of the toxin group. The molecular structure of the toxin are reminiscent of the purine base adenine, and it has been suggested that the toxins might have a physiological function associated with nucleic acid synthesis (Mickelson and Yentsch, 1979). This could explain the variation in cell toxin levels over time that has been reported by White and Maranda (1978). They found that initially high toxin levels fell sharply during mid-log phase of culture growth; this roughly corresponds to the pattern of nucleic acid production in the cell's physiological schedule.

This variation in toxin levels over relatively short time-spans requires that samples of toxin extracts be taken from immediately before and immediately after each grazing session., The toxin molecules are acid-stable, heat-stable, and water-soluble, so the extraction technique capitalizes on these characteristics. A known number of cells are collected by gravity filtration and boiled gently in 0.1 NHCl for about 10 minutes, then the solution is adjusted to pH 3.5 by drop-wise addition of 0.1. NaOH (White and Maranda, 1978). Cell debris is cleared from the solution by centrifugation. The toxin-bearing supernatant is decanted into glass vials, sealed, and sent to a federal laboratory in Ottawa for mouse bioassays (Horwitz, 1975).

Luminescence

Gonyaulax tamarensis is luminescent by virtue of a luciferin-luciferase system comparable to that of fireflies. The dinoflagellate exhibits a pronounced diel variation in its luminescent capacity. The high luminescent scotophase occurs during the night and the weakly luminescent photophase during the day (Sweeney and Hastings, 1957).

This alternation between scottophase and photophase has been utilized by several investigators to characterize the influence of luminescence on copepod grazing behaviour (Esaias and Curl, 1972, White H.,1979, Buskey et al. 1983). These studies show a consistent, negative, effect: ingestion rates on highly luminescent cultures are lower than ingestion rates on weakly luminescent cultures.

The experimental determinations of luminescent capacity in the studies cited above were accomplished using equipment based on the system developed by Biggley et al. (1969), in which luminescence is stimulated mechanically by stirring or bubbling. Because the focus of the present study is on toxicity rather than luminescence, only relative measurements of luminescence are required, in order to generate a correction factor that can be applied to the copepod ingestion rates. Therefore, luminescence measurements are made using an ATP photometer, with culture samples stimulated by injections of 60 mM acetic acid (Schmidt et al., 1978). The measurements obtained are in units of counts per minute, and need to be corrected for the number of cells in the sample to obtain units of counts per cell per minute.

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SPECIES COMPOSITION AND ABUNDANCE OF HARPACTICOID COPEPODS ON INTERTIDAL MACROALGAE, *FUCUS VESICULOSUS* AND *ASCOPHYLLUM NODOSUM*, OFF NOVA SCOTIA, CANADA

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Abstract: Harpacticoid copepods were a numerically important component of epifaunal assemblages of intertidal brown algae off Nova Scotia, representing 41 to 76% of the epifauna of *Fucus vesiculosus* and 26 to 73% of the epifauna of *Ascophyllum nodosum* over one year (May 1983 - May 1984). The abundance of harpacticoids showed similar seasonal fluctuations for both macroalgal species and was positively correlated with epiphyte abundance. Eighteen species or multispecies groupings of harpacticoids from nine families were identified. Species of the genera *Tisbe*, *Mesochra*, and *Heterolaophonte* were most abundant. The harpacticoid fauna corresponds closely to that reported for *A. nodosum*, *F. vesiculosus*, and *Fucus serratus* in Europe.

INTRODUCTION

Marine macroalgae support diverse microbial, epifloral, and epifaunal assemblages (Sieburth et al., 1974; Cundell et al., 1977; Coull et al., 1983). Harpacticoid copepods may represent a major component of these assemblages and an important trophic link between microbial and epifloral films and higher trophic levels including fish and macroinvertebrates (Roland, 1978; Hicks and Coull, 1983). However, there have been few studies of epifaunal assemblages of macroalgae in North America and, with the exception of studies by Gunnill (1982a and b, 1983) and Coull et al., (1983), quantitative information on phytal harpacticoids is lacking.

This study is part of a broader investigation of epifaunal assemblages of two dominant intertidal macroalgae, *Fucus vesiculosus* and *Ascophyllum nodosum*, in a small bay on the eastern shore of Nova Scotia, Canada. Results pertaining to the harpacticoid copepod component of these assemblages, including species composition, relative abundance and seasonal variation, are presented here.

MATERAILS AND METHODS

Epifauna of *Ascophyllum nodosum* and *Fucus vesiculosus* were sampled bimonthly between May 1983 and May 1984 in a moderately exposed embayment at Lower Prospect, Nova Scotia. Three specimens of each macroalgal species were collected from radom locations along a 50 m transect at approximately 0.1 m above the mean low water shortly after exposure at low tide. Individual specimens were placed in plastic bags and preserved in 5% formaldehyde solution. Epifauna were washed from the macroalgae (with filtered seawater) through 0.5 and 0.063 mm sieves and hand sorted under a dissecting scope. The fraction retained on the 0.50 mm sieve was sorted entirely. The fraction retained on the 0.063 mm sieve was subsampled in May, July, and September, 1983 and May, 1984; all other samples were sorted entirely. Replicate subsamples (1/20 volume) were taken using a large bore automatic pipette. Counts of all taxa for five replicate subsamples from initial samples in May 1983 were checked for agreement with a Poisson series (χ^2, $p < 0.05$) indicating random sampling (Elliott, 1977). Subsequently, enough subsamples were sorted to include at least 200 copepods (usually 1 to 3 subsamples). Abundance of other taxa are based only upon the subsamples counted for copepods.

Epiphytic algae were scraped from A. nodosum and F. vesiculosus with a scalpel. Epiphytes and macroalgal specimens were dried separately to a constant weight at 60°C. Numbers of copepods and other epifauna are expressed per 100 grams dry weight of macroalgae. Adult copepods and copepodites are identified to species where possible; copepod nauplii are pooled.

RESULTS

Harpacticoid copepods and their nauplii, nematodes, and halacarid mites were the most abundant components of the epifaunal assemblages of both F. vesiculosus and A. nodosum (Figures 1 and 2, Table 1). Other numerically less important components include polychaetes, molluscs, ostracods, isopods, and amphipods. Abundance of all taxa was highest in July and declined throughout the fall and winter. Abundance of copepod nauplii exceeded that of adults and copepodites in all months except July on F. vesiculosus and July, November and January on A. nodosum.

Table 1. *Mean abundance and standard deviations (in parenthesis) per 100 g dry weight of major faunal taxa on Fucus vesiculosus and Ascophyllum nodosum at Lower Prospect, Nova Scotia.*

Fucus vesiculosus

	May	July	Sept.	Nov.	Jan.	March	May
Turbellaria	1307 (2063)	5854 (4006)	183 (78)	25 (22)	1 (1)	3 (3)	19 (19)
Nematoda	51871 (40784)	22056 (18587)	402 (356)	72 (62)	59 (30)	184 (260)	873 (879)
Halacaridae	7136 (2324)	15115 (3847)	1846 (665)	90 (38)	50 (44)	304 (190)	681 (397)
Harpacticoida	12838 (11929)	22861 (14734)	828 (627)	120 (59)	138 (57)	131 (87)	1060 (1502)
Nauplii	112907 (111507)	10076 (4387)	1584 (953)	205 (223)	195 (77)	437 (150)	4607 (7043)
Diptera	1008 (776)	1447 (1125)	18 (11)	1 (1)	0	0	2 (3)
Others	630 (448)	1617 (701)	168 (44)	56 (25)	138 (105)	111 (141)	216 (109)
Total	187690 (167593)	79114 (42153)	5030 (1957)	568 (247)	582 (64)	1171 (685)	7459 (9693)

Ascophyllum nodosum

	May	July	Sept.	Nov.	Jan.	March	May
Turbellaria	177 (260)	5868 (5839)	2492 (1592)	160 (160)	7 (9)	31 (24)	17 (19)
Nematoda	10683 (15341)	18295 (12010)	1682 (1001)	95 (47)	23 (3)	68 (46)	9953 (4248)
Halacaridae	8328 (13186)	8853 (1412)	1771 (1594)	346 (347)	18 (6)	141 (198)	427 (352)
Harpacticoida	1508 (1972)	18712 (5009)	3709 (2220)	221 (93)	159 (93)	71 (47)	1410 (188)
Nauplii	5575 (8329)	6277 (1730)	4680 (2842)	117 (66)	51 (16)	168 (74)	6552 (1711)
Diptera	252 (329)	1633 (77)	163 (141)	2 (3)	0	1 (1)	14 (12)
Others	138 (129)	1425 (584)	290 (77)	99 (103)	26 (7)	25 (18)	224 (100)
Total	26616 (39540)	61068 (8988)	14811 (8174)	1076 (458)	284 (125)	506 (332)	18596 (4779)

Harpacticoid copepods represented 41.0 to 76.0% (6.8 to 28.9% if nauplii are excluded) of the epifauna of F. vesiculosus and 26.6 to 73.7% (5.7 to 55.9% if nauplii are excluded) of the epifauna of

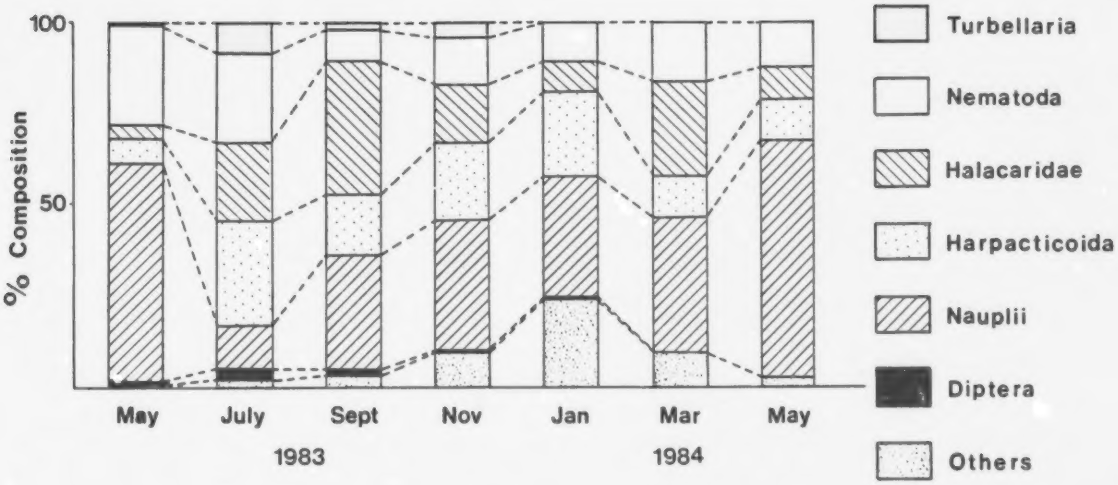

Figure 1. *Percent composition of the major faunal taxa on* F. vesiculosus *collected at Lower Prospect, Nova Scotia.*

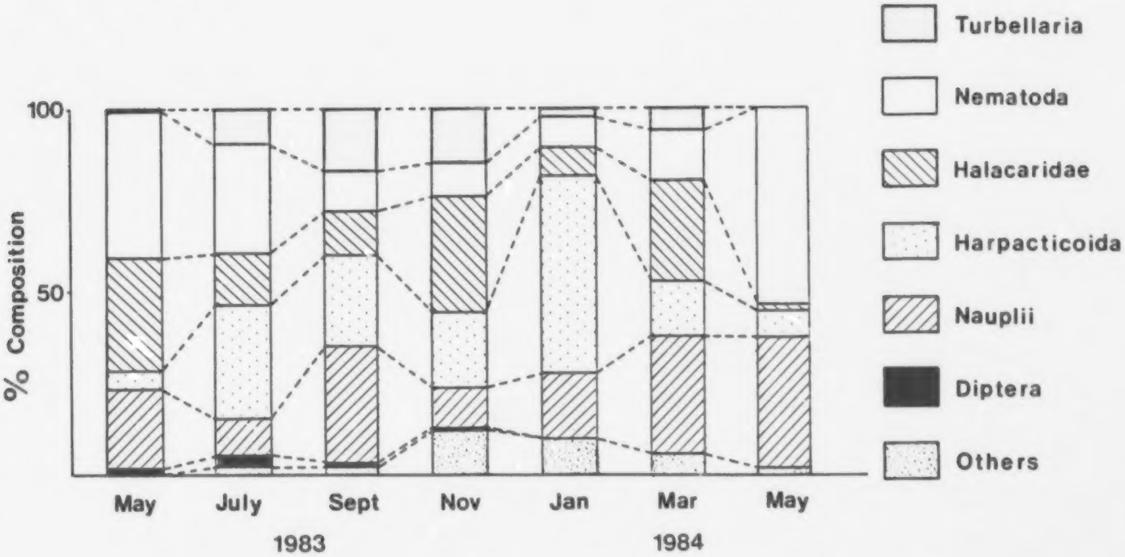

Figure 2. *Percent composition of the major faunal taxa on* A. nodosum *collected at Lower Prospeczt, Nova Scotia.*

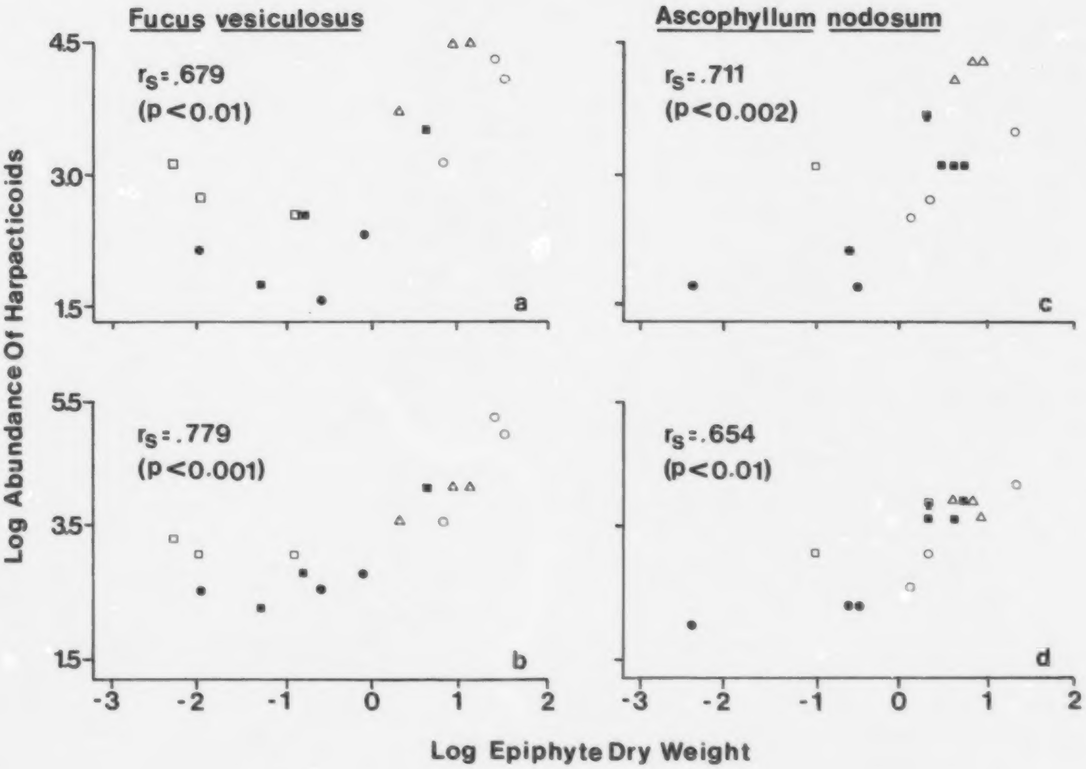

Figure 3: *a and c: Relationships between log adult (and copepodite) abundance and log epiphyte dry weight (per 100 g of macroalgae).*

b and c: relationship between log nauplii abundance and log dry weight (per 100 g of macroalgae).

r_s is the Spaerman rank correlation coefficient.

Year 1983: hollow circles, May; hollow triangles, July; hollow squares, September.
Year 1984: solid circels, March; solid squares, May.

A. nodosum. The abundance of harpacticoid copepods was positively correlated with the dry weight of epiphytes (per 100 grams dry weight of macroalgae) for both F. vesiculosus and A. nodosum (Figure 3).

Eighteen species or multispecies groupings of harpacticoid copepods from nine families are identified from both F. vesiculosus and A. nodosum (Tables 2 and 3). In the genus Heterolaophonte, only adults of Heterolaophonte discophora Willey are identified to species. The grouping Heterolaophonte spp. possibly consists of two species differing in the shape of their fifth thoracic leg, stoutness of leg segments, and setation on the inner surfaces of the P2 to P4 exopods. The setation within this group is variable; many individuals are asymmetrical in setation or intermediate between forms. Copepodites of the genus Heterolaophonte were indistinguishable at the species level and are pooled. Those species which did not correspond to published species descriptions are designated with numbers.

The harpactocoid epifauna of F. vesiculosus and A. nodosum showed similar fluctuations in species abundance throughout the year (Tables 2 and 3). Abundance of most species was highest in July, and declined throughout the winter. Nitocra typica and Mesochra sp. 2 were most abundant in September. Abundance of Tisbe sp. was relatively constant throughout the year on F. vesiculosus but variable on A. nodosum. Dominant during the period of maximal harpacticoid abundance in July, Heterolaophonte spp. accounted for 71.8% and 56.2% of harpacticoids on F. vesiculosus and A. nodosum respectively; Mesochra sp. 2 accounted for 21.7% and 43.8% respectively. During the period of minimal harpacticoid abundance in January, Tisbe sp. accounted for 80.2% and 53.1% of harpacticoids on F. vesiculosus and A. nodosum respectively.

DISCUSSION

Harpacticoid copepods and their nauplii were the most abundant components of the epifaunal assemblages of A. nodosum and F. vesiculosus at Lower Prospect, Nova Scotia. Declines in abundance of harpacticoid copepods in winter may be related to low temperatures. Water temperatures ranged from 18.7°C in July to -1.0°C in January. Freezing of the surface layers of the macroalgal bed can occur during tidal exposure in winter. Lower faunal abundances on subtidal Fucus serratus in Denmark were attributed to low water temperatures (Hagerman, 1966).

Harpacticoid copepod abundance was positively correlated with epiphyte abundance. Epiphytic macroalgae and associated microflora (diatoms, bacteria, and yeasts) may provide microhabitats and food resources for copepods and/or a refuge from predation. Coull and Wells (1983) showed that structural complexity of habitat may be important in reducing fish predation on phytal harpacticoid copepods.

The families Harpacticidae, Tisbidae, and Thalestridae are among the most abundant of phytal harpacticoid copepods (Hicks, 1977). The families Ectinosomatidae, Parastenheliidae, Ameiridae, Canthocamptidae, and Laophontidae are more characteristic of sediment biotopes (Hicks, 1977), although several species of these families are also abundant on A. nodosum, F. vesiculosus, and F. serratus (Colman, 1939; Ohm, 1964; Hagerman, 1966; Hicks, 1980). The species composition of harpacticoids reported here corresponds closely to assemblages on F. vesiculosus and A. nodosum in Britain (Colman, 1939), and F. serratus in Germany (Ohm, 1964), Denmark (Hagerman, 1966) and Britain (Hicks, 1980). Only Microsetella and Pseudonychocamptus were not found in these previous studies.

The high degree of variability in abundance of harpacticoid copepods among individuals of F. vesiculosus and A. nodosum indicates a patchy spatial distribution. Patchiness may be related to differences

Table 2. *Mean abundance and standard deviations (in parenthesis) per 100 g dry weight and, percent composition of harpacticoid copepods on Fucus vesiculosus at Lower Prospect, Nova Scotia.*

	May	July	Sept.	Nov.	Jan.	March	May
Ectinosomatidae							
Microsetella norvegica	499 (413) 3.9%	0	32 (24) 3.8%	0	0	2 (2) 1.7%	1 (1) 0.1%
Harpacticidae							
Harpacticus sp. 1	0	0	0	5 (5) 4,3%	2 (3) 1.4%	0	0
Harpacticus sp. 2	787 (431) 6.1%	8 (13) 0.1%	2 (2) 0.2%	3 (3) 2.8 %	0	13 (14) 10.0%	902 (1406) 85.0%
Harpacticus sp. 3	15 (25) 0.1 %	0	0	0	0	0	0
Zaus abbreviatus	8. (7) 0.1%	0	0	0	10 (9) 7.3%	7 (5) 5.5%	0
Tisbidae							
Tisbe sp.	74 (127) 0.6%	100 (102) 0.4%	71 (107) 8.5%	71 (65) 58.9%	111 (51) 80.2%	69 (55) 52.7%	25 (36) 2.4%
Thalestridae							
Thalestris purpurea	78 (124) 0.6%	1180 (1394) 5.2%	364 (399) 43.8%	9 (11) 1.7%	0	2 (0) 1.3%	1 (2) 0.1%
Parathalestris sp.	37 (64) 0.3%	0	0	0	1 (1) 0.5%	0	0
Diarthrodes major	1240 (2110) 9.7%	46 (80) 0.2%	0	0	0	2 (2) 1.6%	1 (1) 0.1%
Parastenheliidae							
Parastenhelia spinosa	110 (110) 0.9%	0	4 (5) 0.5%	8 (10) 6.9%	4 (5) 2.9%	0	5 (7) 0.5%
Diosaccidae							
Amphioascopsis sp.	0	0	0	0	0	2 (2) 1.3%	4 (8) 0.4%
Ameiridae							
Nitocra typica	37 (64) 0.3%	69 (69) 0.3%	190 (207) 22.8%	4 (6) 3.1%	4 (7) 2.9%	8 (12) 6.1%	14 (1) 1.3%
Canthocamptidae							
Mesochra sp. 1	37 (64) 0.3%	0	74 (88) 8.9%	15 (4) 12.4%	5 (3) 3.4%	3 (3) 1.9%	3 (3) 0.3%
Mesochra sp. 2	1700 (1420) 13.3%	4951 (5031) 21.7%	12 (17) 1.5%	0	0	5 (2) 3.9%	38 (48) 3.6%
Laophontidae							
Pseudonychocamptus koreni	199 (250) 1.5%	0	0	0	0	11 (17) 8.1%	0
Heterolaophonte discophora (adults only)	1205 (1022) 9.4%	814 (1326) 3.6%	0	0	0	3 (4) 2.4%	1 (1) 0.1%
Heterolaophonte spp.	588 (454) 4.6%	6091 (4785) 26.6%	60 (61) 7.1%	1 (1) 1.0%	2 (3) 1.4%	4 (5) 2.8%	33 (29) 3.1%
Heterolaophonte spp. juv.	5918 (6374) 46.1%	9510 (7907) 41.6%	18 (24) 2.1%	3 (2) 2.5%	0	1 (1) 0.4%	32 (33) 3.1%
Unidentified	302 (338) 2.4%	92 (159) 0.4%	6 (11) 0.7%	1 (1) 0.5%	0	1 (1) 0.4%	0

Table 3. *Mean abundance and standard deviation (in parenthesis) per 100 g dry weight and, percent composition of harpacticoid copepods on Ascophyllum nodosum at Lower Prospect, Nova Scotia.*

	May	July	Sept.	Nov.	Jan.	March	May
Ectinosomatidae							
Microsetella norvegica	28 (38) 1.8%	0	0	0	2 (1) 1.0%	2 (2) 3.5%	11 (10) 0.8%
Harpacticidae							
Harpacticus sp. 1	18 (31) 1.2%	5 (8) <0.1%	0	1 (1) 0.1%	1 (0) 0.5%	0	0
Harpacticus sp. 2	95 (161) 6.3%	1 (1) 0.1%	0	1 (1) 0.3%	0	3 (4) 4.4%	182 (245) 12.9%
Harpacticus sp. 3	8 (3) 0.5%	0	0	0	0	0	0
Zaus abbreviatus	6 (10) 0.1%	0	0	0	1 (1) 0.4%	2 (1) 2.6%	2 (4) 0.2%
Tisbidae							
Tisbe sp.	6 (11) 0.4%	315 (352) 1.7%	46 (18) 1.2%	27 (9) 12.2%	84 (54) 53.1%	9 (5) 13.4%	36 (23) 2.6%
Thalestridae							
Thalestris purpurea	18 (3) 1.2%	0	26 (27) 0.7%	4 (3) 1.7%	0	0	5 (5) 0.3%
Parathalestris sp.	2 (4) 0.2%	5 (8) 0.1%	0	0	1 (1) 0.6%	1 (1) 0.3%	0
Diarthrodes major	59 (102) 3.9%	10 (17) 0.1%	0	0	0	1 (1) 1.8%	15 (19) 1.1%
Parastenheliidae							
Parastenhelia spinosa	0	65 (62) 0.4%	208 (47) 5.6%	8 (9) 3.8%	1 (1) 0.3%	2 (3) 2.7%	0
Diosaccidae							
Amphiascopsis sp.	2 (4) 0.2%	10 (17) 0.1%	84 (100) 2.3%	0	0	2 (2) 3.2%	16 (6) 1.1%
Ameiridae							
Nitocra typica	19 (25) 1.2%	164 (198) 0.9%	428 (70) 11.6%	117 (71) 52.6%	19 (16) 11.8%	13 (10) 19.1%	2 (4) 0.2%
Canthocamptidae							
Mesochra sp. 1	31 (53) 2.0%	66 (19) 0.4%	150 (35) 4.0%	50 (27) 22.5%	36 (20) 22.9%	8 (4) 11.1%	21 (8) 1.5%
Mesochra sp. 2	509 (616) 33.7%	8179 (981) 43.8%	1424 (1096) 38.4%	5 (4) 2.1%	14 (20) 8.7%	18 (24) 25.1%	646 (216) 45.8%
Laophontidae							
Pseudonychocamptus koreni	1 (2) 0.1%	0	0	3 (6) 1.5%	1 (2) 0.7%	1 (1) 1.1%	0
Heterolaophonte discophora (adults only)	159 (234) 10.5%	101 (92) 0.5%	24 (41) 0.7%	0	0	3 (5) 5.0%	13 (9) 1.0%
Heterolaophonte spp.	317 (481) 21.0%	4340 (543) 23.3%	848 (709) 22.9%	3 (2) 1.5%	0	4 (4) 6.2%	60 (55) 4.2%
Heterolaophonte spp. juv.	233 (313) 15.4%	5359 (3894) 28.8%	461 (356) 12.4%	3 (2) 1.2%	0	0	396 (112) 28.1%
Unidentified	0	0	8 (7) 0.2%	1 (1) 0.3%	0	1 (1) 0.5%	2 (4) 0.2%

in the composition and abundance of microbial surface films among macroalgae which, in turn, may be associated with differences in the age or physiological state of the macroalgae (Cundell et al., 1977). Changes in the fauna of F. serratus (Hagerman, 1966) and Pelvetia fastigiata (Gunnill, 1983) were associated with changes in the reproductive cycle of the macroalgae. Interactions between harpacticoid species and other members of the macroalgal assemblages also may effect distribution.

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THE POPULATION OF PLANKTONIC COPEPODS IN TWO AREAS OF SARONICOS GULF (GREECE): POPULATION DYNAMICS, CONTRIBUTION TO SECONDARY PRODUCTION, AND RELATION TO THE PRINCIPAL OCEANOGRAPHIC PARAMETERS

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Abstract: The copepod populations of two areas of Saronicos Gulf (Greece) have been studied from plankton samples taken by WP2 net in oblique hauls. Station 1 was located at Selinia, a small gulf of Salamina Island, at a distance of about 5 km from the sewage outfall of Athens and Piraeus, and Station 2 about 20 km southwards at the entrance of the small Gulf of Vouliagmeni. Copepods were the dominant zooplankton at both stations with animal mean of 43.49% of the total zooplankton in number for Station 1 and 63.59% for Station 2. *Acartia clausi* was the most important copepod species at both stations, followed by *Centropages typicus* and *Temora stylifera*. Although Station 1 presented characteristics of polluted and eutrophic waters, with low species diversity (about 20 copepod species identified compared with 40 from Station 2), the zooplankton biomass was low. It is believed that this situation is due to the presence of high concentrations of phytoplankton. Temperature is the main ecological factor controlling the abundance of copepods in the studied area.

INTRODUCTION

Saronicus Gulf is an area of primary importance for Greece because its coastal area includes an important part of the population and industry of the country. Although during the last 15 years most marine biological research in Greece has concerned this area, the ecosystems of Saronicos cannot be considered as well understood. This is mainly due to fragmentary research activity, lack of systematic and multidisciplinary surveys, peculiar environmental conditions (turbulent movements and complex current systems), and pollution. Furthermore the continuous addition of pollutants into the Saronicos ecosystems results in a progressive modification of the community structures. Pollution sources are found in various parts of Saronicos but mainly in its northeastern area where the main sewage outfall of the metropolitan complex of Athens, many industries, and Piraeus harbour are located.

This paper concerns the results of a systematic survey of zooplankton in two areas of Saronicos which have been studied only occasionally.

MATERIAL AND METHODS

Figure 1 shows the sampling area and the collection stations. Station 1 (S1) is located in the northeastern part of the gulf at Selinia, a small gulf of the Salamina Island strongly influenced by the sewage outfall situated about 5 km away. Station 2 (S2) is located about 20 km to the south at Vouliagmeni. Here the influence of the main pollution sources from the north is strongly reduced and is generally considered unpolluted. However, a source of pollution is developing locally: the Vouliagmeni summer resort with its small touristic harbour. Due to the closed nature of the area the renewal of waters is limited so that the development of eutrophic and polluted conditions is favoured.

Samples were collected by oblique hauls from bottom to surface with a WP2 net (220 μ) equipped

Table 1. *Annual range and mean (x) of oceanographic parameters at Station 1 and 2*

Station	Temperature °C	Salinity ‰	Dissolved oxygen ml/l	Water transparency m
1	13.00 - 25.20	37.07 - 38.34	1.50 - 7.21	2 - 18.20
	x = 19.57	x = 37.75	x = 4.87	x = 6.95
2	12.80 - 24.60	36.82 - 38.43	2.04 - 6.32	13 - 30.00
	x = 19.19	x = 37.91	x = 4.84	x = 20.42

Table 2. *Annual range and mean (x) of biomass values per cubic meter expressed as wet weight, dry weight and organic matter content.*

Station	Wet weight (mg)	Dry weight (mg)	Organic matter (mg)
1	0.38 - 156.35	1.87 - 7.50	0.00 - 2.16
	x 53.26	x 3.68	x 0.56
2	16.67 - 449.31	1.12 - 45.3	0.06 - 5.39
	x 135.72	x 9.49	x 1.44

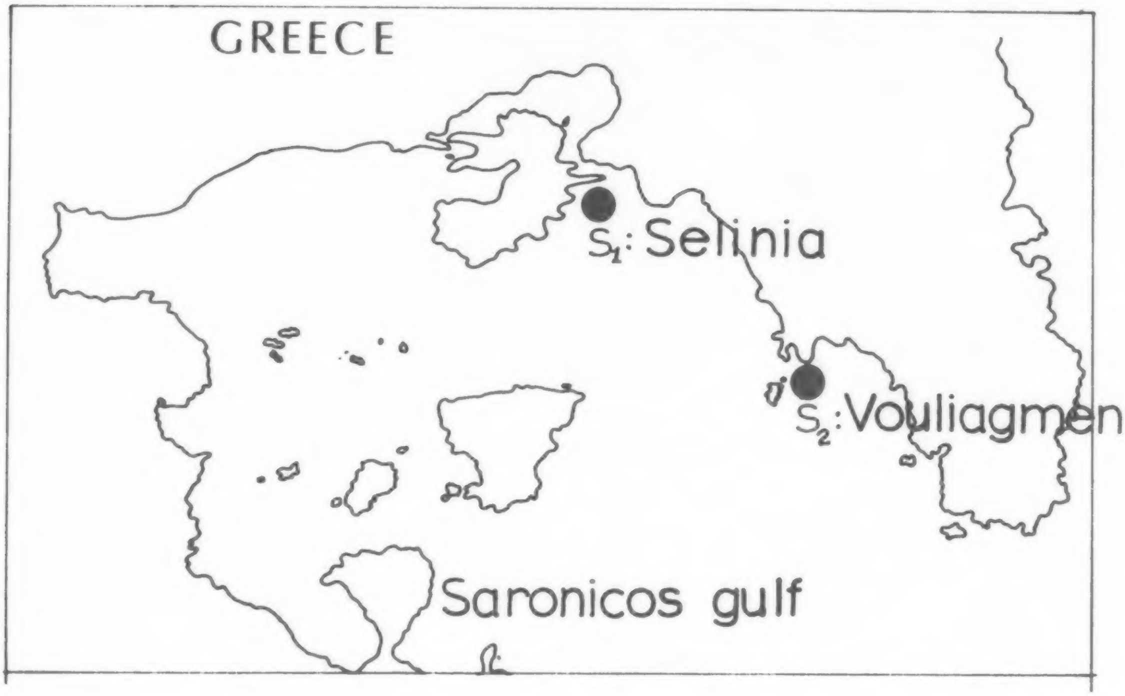

Figure 1. *The sampling area and the collection stations.*

with a T.S.K. flowmeter. The sampling stations were visited monthly at the same hour of the morning. Simultaneous measurements of the principal oceanographic parameters (temperature, salinity, dissolved oxygen, and water transparency) were also taken. Samples were fixed in 4% neutralized formalin. Subsamples were obtained using a Folsom plankton splitter.

In order to characterize the Copepoda as a whole and also of the main copepod species, we have proceeded in a statistical elaboration of the results using regression analysis. The factors used in the analysis were temperature, salinity, dissolved oxygen, and water transparency. These were treated as main effects (linear regression analysis) and as elements in interaction (multilinear regression analysis). Since these are not causative factors the analysis is simply a descriptive one.

RESULTS AND DISCUSSION

Table I summarizes measurements of the oceanographic parameters at the two stations.

Means and ranges of temperature, salinity and dissolved oxygen showed no significant differences between the two stations. On the contrary water transparency showed a significant difference between the two stations (t 10.8019, v 13 as tested by t-test). The waters at Vouliagmeni were much more transparent. The reduced water transparency at Selinia my be attributed to the very dense concentrations of the phytoplankton in this area (Ignatiades, pers. comm.). Salinity and temperatures are somewhat lower than the usual for Saronicos Gulf (Moraitou-Apostolopoulou, 1974). Similar lower salinity values have previously been measured at Keratsini, adjacent to S1 area, in the vicinity of the outfall (Moraitou-Apostolopoulou and Kiortsis, 1976).

Figure 2 shows the annual cycle of biomass, expressed as numbers of individuals per cubic meter, for the two stations. Table 2 summarizes the results of biomass measurements expressed as wet weight, dry weight and organic matter content.

Not all samples were taken into consideration for the calculation of biomass. Two samples at S1 and four at S2 which had unusual biomass values had clogged flowmeter. At S1 this was observed at the sampling of 1983-04-21 and was due to very large population of *Noctiluca miliaris*. The total biomass in dry weight of a 5-minute sample was 39.55 compared with 0.08 to 7.50 mg of other samples of a similar time duration. The other case was observed on 1983-01-14 when a sample biomass of 55.93 was measured and was due to high number of appendicularians.

At S2 a sample with an exceptional high biomass of 1013.93 mg was observed on 1983-06-25. This sample contained a very dense concentration of cladocerans but also a large number of appendicularians and doliolids. A similar biomass value (1090.63 mg) was noted on 1982-02-04 due to high numbers of chaetognaths. The high sample biomass of 1983-05-31 (45.30 mg) was due to very high numbers of cladocerans and of some large zooplankters such as doliolids and appendicularians. Large zooplankton such as siphonophores and appendicularians were also found in the sample of 1982-12-07 when high biomass (283.64 mg) was also measured.

The mean biomass of S1 was 1576 ind/m^3 and for S2 1016 ind./m^3. From the above it becomes clear that the calculated biomass values are lower than the real ones and this is true especially for S2 where in four cases very high plankton biomass were found and because of the blocking of the flowmeter these stations could not be taken into consideration.

The fact that S1 has lower biomass values than those of S2 is striking. High biomass values were expected at S1 because of nutrient enrichment from the sewage and very dense populations of

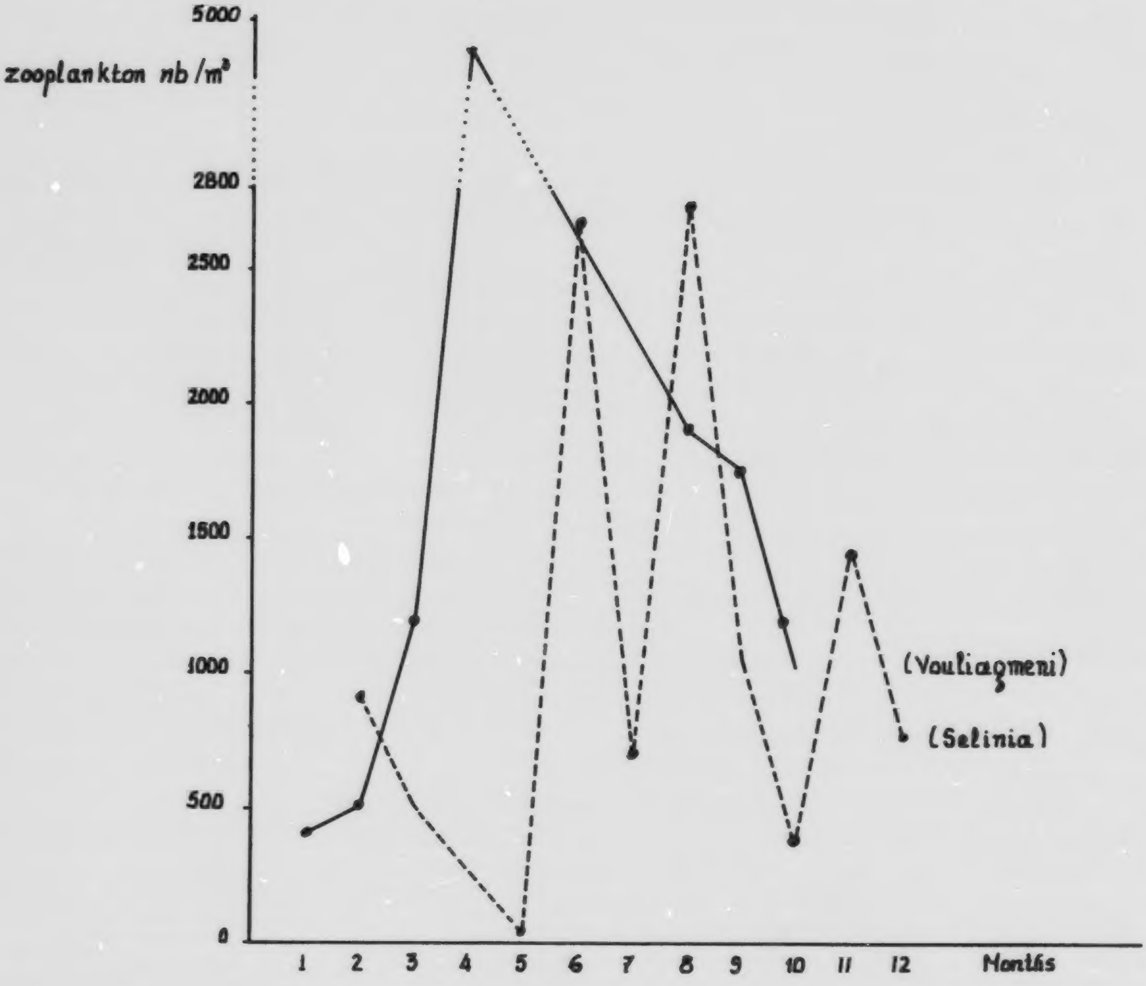

Figure 2. *Annual cycle of biomass (number of individuals per cubic meter) in the two sampling stations.*

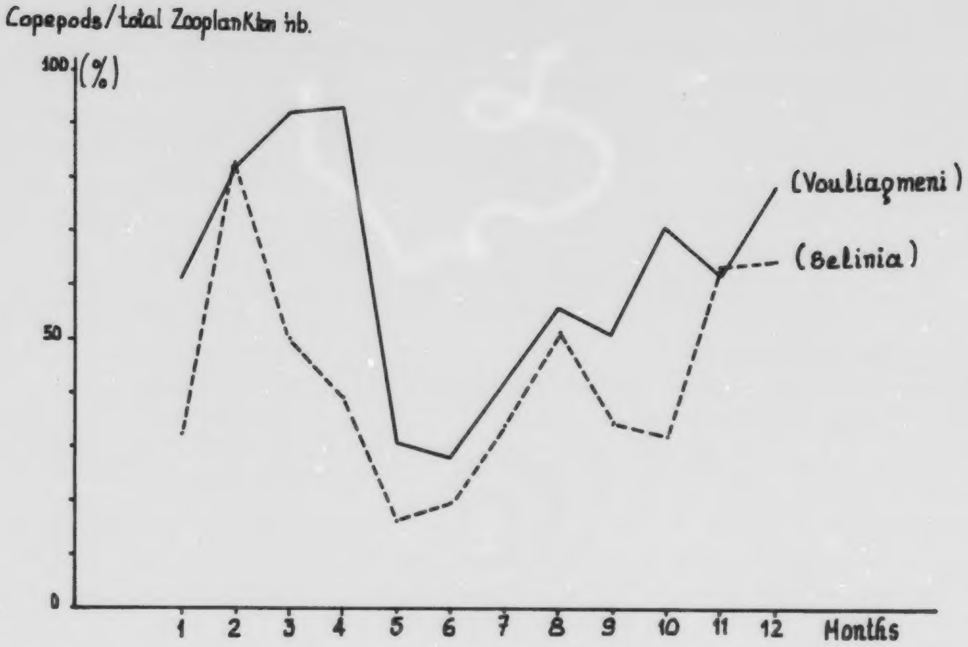

Figure 3. *Annual cycle of copepods (percentages to the total zooplankton numbers) in the two sampling stations.*

Table 3. *Multilinear regression analysis between copepod abundance and factors of interaction with significant* R^2. $z = a_0 + a_1x + a_2y$

Station	Period	Factors	Regression equation	R^2
1	182-10-21 to 1983-01-12	Temperature X Transparency	$z = 36.52 - 0.058x - 1.39x$	0.921
	ditto	Transparency X Dissolved oxygen	$z = 0.638 - 0.36x + 0.403y$	0.9803
	1983-05-20 to 1983-10-12	Transparency X Dissolved oxygen	$z = 7.44 - 0.014x - 0.196y$	0.853
2	1982-12-07 to 1983-05-31	Salinity X Dissolved oxygen	$z = 174.63 - 0.066x + 4.69y$	0.811
	ditto	Salinity X Transparency	$z = 429.32 - 0.077x + 10.80y$	0.890

z = copepod abundance (number of individuals/m^3)

phytoplankton. It is also possible that the large quantity of phytoplankton reduces the filtering rate of zooplankton grazing rate. This was also observed for some periods of the year at Elefsis Bay (Moraitou-Apostolopoulou and Ignatiades, 1980). The zooplankton biomass of S2 can generally be considered somewhat higher than the usual values of south Saronicos (Moraitou-Apostolopoulou, 1981).

Copepods were the dominant zooplankton at both stations with a mean of 43.39 % of all animals collected at S1 and 63.59 % at S2 (Fig. 3). With the exception of cladocerans (mean of 32.55 % at S1 and 14.42% at S2), all other zooplankton groups are of minor importance.

S1 is characterized by lower copepod species diversity (20) than at S2 (40). The species diversity in copepods at S1 is similar to that at Elefsis Bay, a polluted environment situated at the northeastern part of the gulf; and that of S2 is the same as that of south Saronicos (Moraitou-Apostolopoulou, 1981).

The dominance of copepods is greater during the cold period, while during the warm period cladocerans proliferate, reaching high proportions. An exception was noted in the samples collected in March and April at S1 when dense populations of cladocerans, mainly due to Podon intermedius, were found.

Copepod populations were dominated by Acartia clausi, the most important copepod species of Saronicos. Acartia makes an annual mean of 8.53 % and up to a monthly mean of 59.17 % of all animals collected at S1 and 23.36 % and up to 62.36 % at S2. Acartia, a psychrophilic form, abounds in both areas during the cold period (Fig. 4).

Centropages typicus is second in numerical importance among copepod species at S2 with an annual mean of 13.03 % and up to 22.91 in spring. This form is found in reduced numbers at S1 having an annual mean of 3.24 % (Fig. 4).

Temora stylifera, the most dominant copepod species in the Aegean Sea (Moraitou-Apostolopoulou, 1973), forms 4.54 % at S1 and 5.55 % at S2 (Fig. 4).

Other common copepod species are Oncaea media, Oithona nana, O. plumifera, Clausocalanus furcatus and Paracalanus parvus at S1 and O. plumifera, O. nana, C. furcata and P. parvus at S2. An abundant element of copepod population are the various copepodid stages, most of them P. parvus.

The regression equation for all factors have been calculated separately for the three thermal hydrographic periods (cold, interemediate, warm). The regression equations for temperature are as follows: $y = b - mx$, where y = copepod abundance (number per cubic meter), and x = temperature (C^o).

Station	Period	Regression equation	r
1	1982-10-21 to 1983-01-14	$y = 18.27 - 0.08x$	0.046
	1983-01-14 to 1983-05-20	$y = 23.94 - 0.41x$	-0.81*
	1983-05-20 to 1983-10-21	$y = 20.62 + 0.156x$	0.912*
2	1982-12-07 to 1983-05-31	$y = 19.84 - 0.19x$	-0.925*

All coefficients of correlation marked by an asterisk are significant at 0.05 level. The coefficients of correlation of salinity, dissolved oxygen and water transparency (not shown here) were in all cases not significant.

The multilinear regression analysis showing the interaction of factors on copepod abundance gave significant coefficients of determination for a limited number of cases (Table 3).

The same procedures (linear regression analysis, multilinear regression analysis) were followed for the abundance of the three most dominant copepods, Acartia clausi, Centropages typicus, and Temora

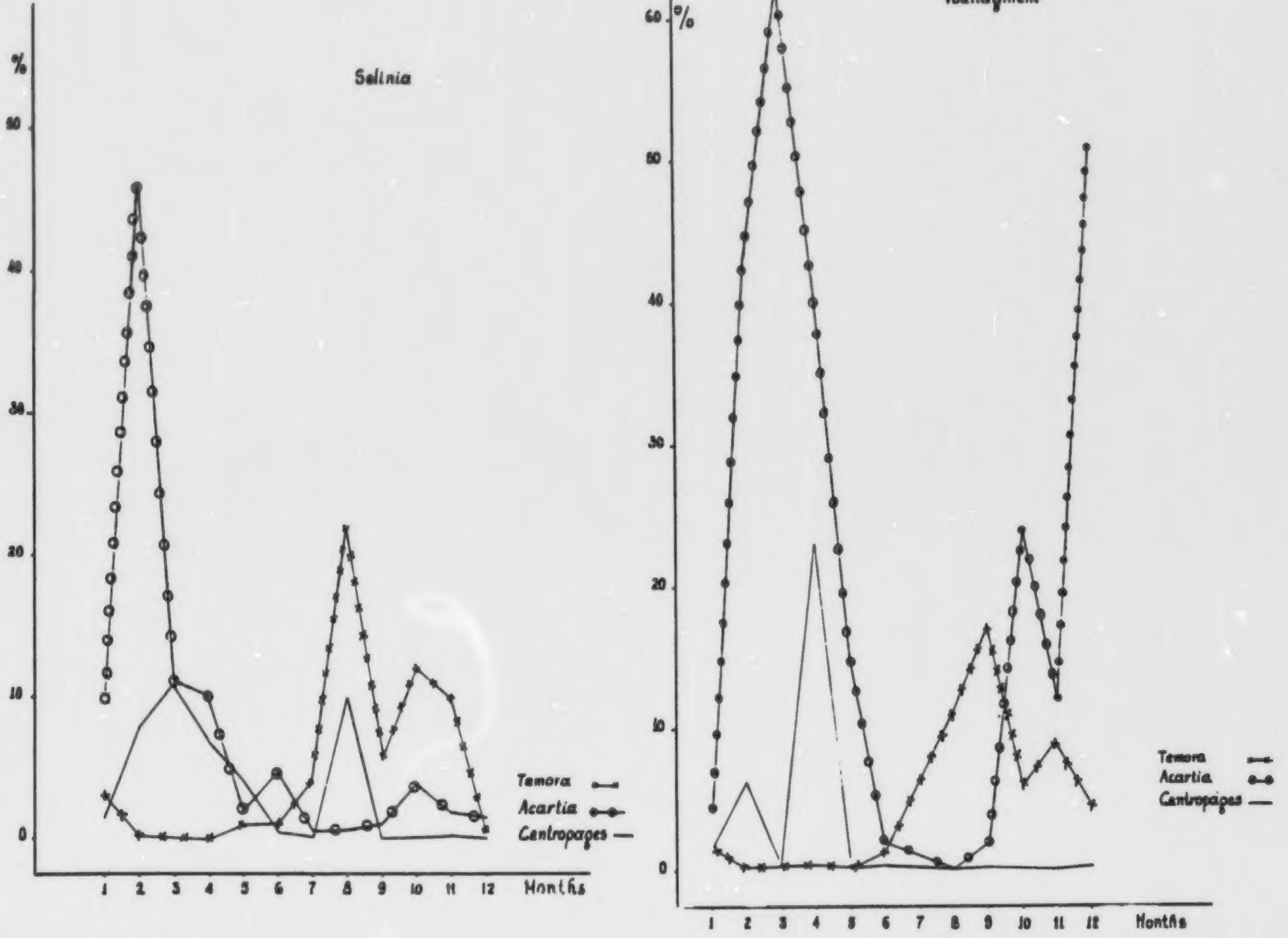

Figure 4. *Annual cycle of the three most important copepod species (percentage to the total zooplankton numbers) in the two stations.*

Table 4. *Linear relations between copepod species abundance and environmental factors (0.05 level).*

stage	Station	Period	Factor (X)	Regression equation	r
1. Acartia clausi					
ad.o.	2 1	1983-02-14 to 1983-05-31	Temperature	y = 13.0036 + 0.0030x	0.9960
ad.o.	1	1982-10-21 to 1982-12-08	Temperature	y = 15.96 + 0.9904x	0.9556
ad.o	1	dito	Dissolved oxgen	y = 1.76 + 0.5581x	0.9987
ad.o	1	dito	Salinity	y = 14.25 + 2.574x	0.889
ad.o	1	dito	Transparency	y = -58.25 + 8.913x	0.9201
Copepodid	1	dito	Salinity	y = 36.93 + 0.0736y	0.9396
dito	1	1983-05-20	Temperature	y = 12.72 + 0.009x	0.9715
2. Centropages typicus					
ad.o	2	1983-01-21 to 1983-04-18	Temperature	y = 12.860 + 0.0210x	0.9920
ad.o	2	dito	dito	y = 12.97 + 0.0368x	0.9850
Copepodid	2	dito	dito	y = 12.840 + 0.0017x	0.9890
dito	1	dito	dito	y = 12.960 + 0.015x	0.9796
ad.o	1	1983-01-14 to 1983-04-21	Transparency	y = 3.29 + 0.0358x	0.9571
ad.o	1	dito	Temperature	y = 12.97 + 0.0358x	0.9850
ad.o	1	1983-05-20 to 1983-08-24	dito	y = 24.63 - 7.46x	0.935
3. Temora stylifera					
copepodid	1	1982-10-21 to 1982-12-08	Salinity	y = 36.30 + 0.0118x	1.000
dito	1	1983-01-14 to 1983-04-21	Dissolved oxygen	y = 6.12 - 0.451x	0.9939
dito	1	1983-05-20 to 1983-08-24	Transparency	y = 18.25 + 0.0198x	0.8893

stylifera. The analysis was performed separately on the males, females and copepodids. Using the linear regression, some significant correlations have been found, and these are shown in table 4. From table 4 it can be concluded that temperature is the main ecological factor for *Acartia clausi* and especially *Centropages typicus*

The multilinear regression analysis has shown in the following cases significant correlations of determination:

Factors of interaction	Acartia	Centropages	Temora
temperature X transparency	5+ times	1 time	-
salinity X transparency	2 times	4 times	3 times
temperature X salinity	4 times	-	-
salinity X dissolved oxygen	1 time	-	1 time
temperature X dissolved oxygen	-	1 time	3 time
dissolved oxygen X transparency	-	1 time	1 time

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DESCRIPTION OF THE MALE OF TRACHELIASTES MACULATUS KOLLAR, 1835 (SIPHONOSTOMATOIDA, LERNAEOPODIDAE)

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Abstract: The female Tracheliastes maculatus is a parasite of freshwater bream (Abramis brama) attached to its scales. During the study of females the male was found. It was attached to the posterior end of the female body. The description is based on only one specimen. The male of this species is closely similar to the males of the other species of the genus.

INTRODUCTION

Tracheliastes maculatus Kollar 1835, is a species-specific parasite of the bream, Abramis brama Linnaeus. The females are parasitic; they dwell attached to the fish scales. It occurs in central Europe from Finland to Austria and from Belgium to central Russia (Kozikowska, 1957), sometimes in large quantities and, under certain circumstances, causing substantial economic losses (Grabda and Grabda, 1957). The parasitic copepod has been the subject of numerous papers since its original description. However, I am not aware of any description of the male of this species in the literature.

MATERIAL AND METHODS

In studying the life cycle of T. maculatus, I collected adult females from the bream body surface. Every female was thoroughly examined under a microscope. The study was carried out from August 1983 through March 1984. The fish were at first obtained from Szczecin Lagoon fishermen; in winter I caught them myself from the cooling water channel of the Dolna Odra Power Station. I examined 110 females of T. maculatus. Only one of them (7 November 1983, Dolna Odra) was found to be associated with a male attached to its genital process.

MORPHOLOGY OF THE MALE

Three types of males can be distinguished in the family Lernaeopodidae (Kabata, 1979). The males of Tracheliastes belong to the Type A of Kabata's classification. The body can be divided into two basic parts: the cephalothorax and the genito-abdominal complex (Fig. 1). These two parts are almost equal in length; however, the cephalothorax with its well-developed appendages appears larger. Both parts are arranged along the same plane; when, however, the male was irritated, its posterior part bent under the cephalothorax. The cephalothoracic appendages include two pairs of antennae, a mouth cone with mandibles, two pairs of maxillae, and maxillipeds (Fig. 2). The body is 0.59 mm long and

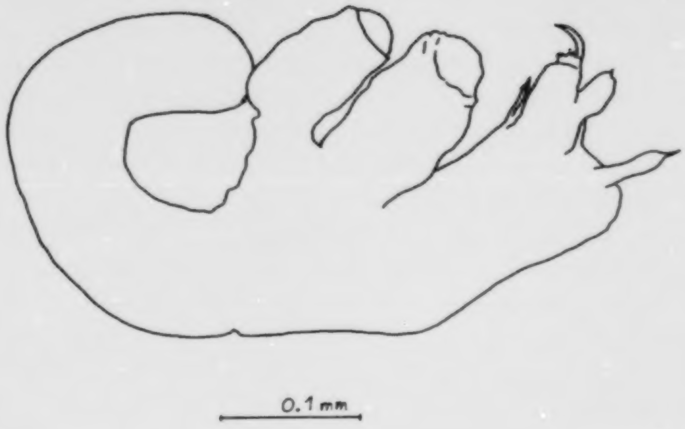

Figure 1. *Tracheliastes maculatus, male (lateral view).*

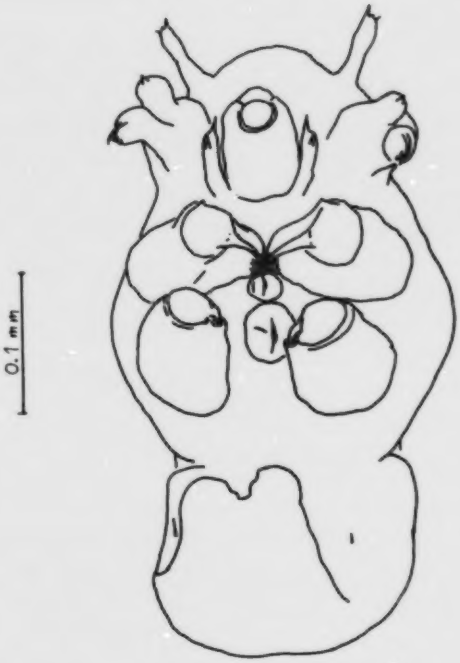

Figure 2. *Tracheliastes maculatus, male (ventral view).*

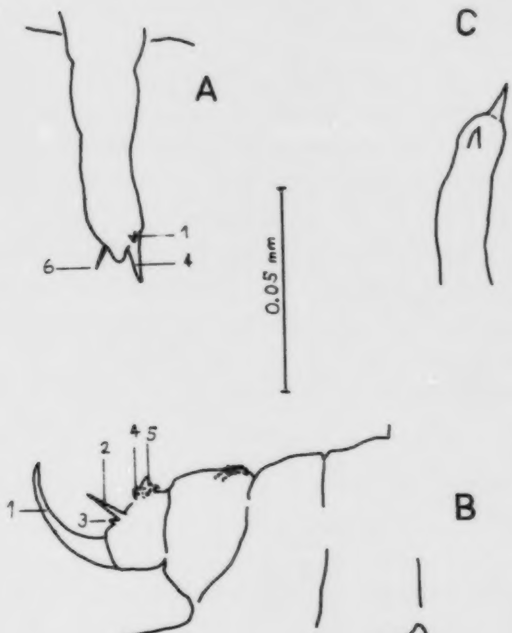
A
1
4
6
C
0.05 mm
4 5
2
1
3
B

Figure 3. *Appendages of Tracheliastes maculatus*
A - First antenna;
B - Second antenna;
C - First maxilla.

0.25 mm broad.

The first antenna is uniramous, with three poorly visible segements (Fig. 3A). The basal is wider than its length. The next segment is somewhat longer, and the third one is clearly elongated and terminated with an apical armature. When describing the latter I am following Kabata's (1979) terminology to render the descriptions comparable. The largest element is a digitiform seta 4, with a small tubercle 1 visible at its base. At the centre of the top of the first antenna there is a short, stout and rounded process of obscure homology. The second long element of the armature is a thin seta 6.

The second antenna is biramous. Sympod is indistinctly 2-segmented. Exopod and endopod are of equal length (Fig. 3B). The exopod consits of a single, bulbous segment provided with a strong process on its end and with some fine denticles on the inner margin near the base of the process. The endopod is 2-segmented, with a well-developed apical armature. The most conspicuous element of the latter is a strong hook 1, its base housing a spine 2 and tubercle 3. The central process 5 of the swelling 4 is surrounded by numerous small denticles. There is a group of minute denticles on the inner margin of the endopod basal segment.

The first maxilla has a poorly visible segmentation and simplified structure (Fig. 3C). It is elongated and tapers towards its distal end, where two processes are present, the longer on the terminal end and the shorter slightly below the longer.

The second maxilla is uniramous and 2-segmented. The proximal segment is large and cylindrical. The small terminal segment tapers rapidly; it terminates with a prominent, long claw. The myxa on the medial margin provides a support for this claw, bending to the inside. This is a typical grasping appendage.

The maxillipeds are similar to the second maxillae in morphology and function. Their shape strongly resembles that of maxillipeds of males of other species of Tracheliastes. The corpus maxillipedi is elongated in lateral view and more squarish when viewed from the rear. Subchela is stout and rounded. The terminal claw is heavy, strong and rapidly curved towards a simple pocket on the inner margin of the maxilliped. The medial process is visible between the maxilipeds. There is a small process which is similar and immediately anterior to the medial process.

The genito-abdominal appendages are two pairs of vestigial appendages in the form of paired setae (Fig. 4). Two genital plates protecting the genital orifices (Fig. 5) are located laterally at the posterior part of the genito-abdominal complex. There are also two semicircular uropods on the end of the body.

DISCUSSION

The genus Tracheliastes contains seven valid species: T. polycolpus Nordmann, 1832, T. longicollis Markevich, 1940, T. maculatus, Kollar 1835, T. sachalinensis Markevich, 1936, T. tibetanus Kuang, 1964, T. mourkii Hoffmann, 1881, and T. gigas Richardi, 1880. So far, males have been described in only three of them: T. polycolpus by Markevich (1937), T. longicollis by Markevich (1940), and T. tibetanus by Kuang (1964). The descriptions of these males are not sufficiently detailed for a thorough morphological comparison of the males of the genus Tracheliastes. Some diffuculty also can be encountered when comparing the details of the appendages of the male of T. maculatus with those of the female. The existing description of the female is also insufficiently detailed.

It is extremely difficult to find a male of T. maculatus attached to an adult female. This is

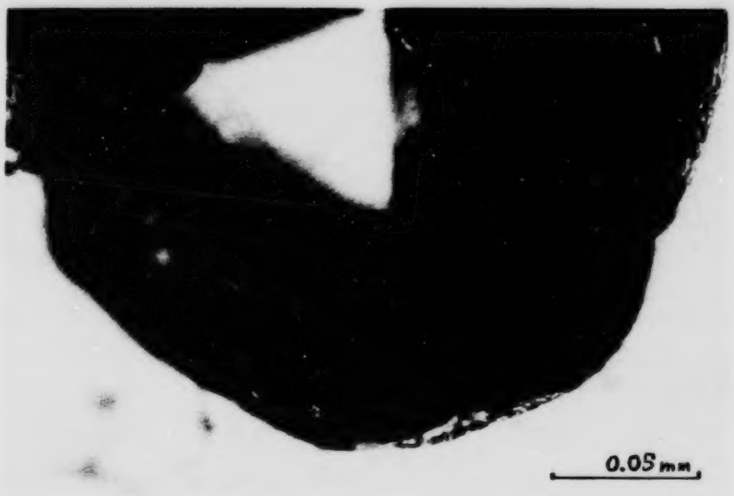

Figure 4. Tracheliastes maculatus - Medial part of the genito-abdominal complex with vestigal legs visible.

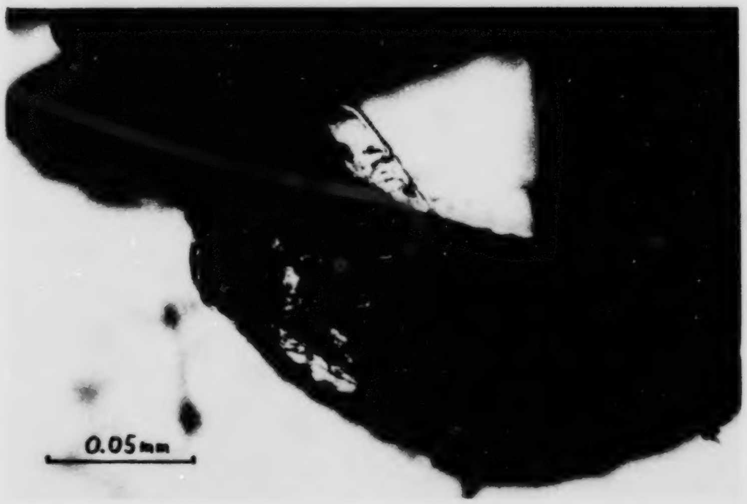

Figure 5. Tracheliastes maculatus - End of body. The genital plate is visible.

presumable because females of some lernaeopodid species are fertilized before they reach sexual maturity, e.g., in Chalimus IV of Salmincola californiensis (Dana 1852) (Kabata and Cousens, 1973). It is probable that this is also the case in T. maculatus.

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EXTRUSION OF THE FILAMENTUM FRONTALE IN COPEPODIDS OF TRACHELIASTES MACULATUS KOLLAR, 1835 (SIPHONOSTOMATOIDA: LERNAEOPODIDAE)

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Abstract: While studying the life cycle of Tracheliastes maculatus special attention was paid to the extrusion of the frontal filament of the copepodids. The frontal filament is an organ of attachment. It appears already in the nauplier stage in the egg. The extrusion of this filament is a complicated hydraulic procedure.

INTRODUCTION

Copepodids of the Siphonostomatoida attach themselves to their hosts by means of a special apparatus which differs morphologically in various taxa of the suborder. The apparatus shows marked differences in morphology even within the same family. Brief descriptions of the organ have been published sporadically in papers on copepod developmental stages. The descriptions are sometimes supplemented with data on modes of attachment (Sproston, 1942; Ho, 1966; Kabata, 1972, 1976; Kabata and Cousens, 1973). The attachment organ, also called the frontal filament, deserves a more detailed description as its form is a key taxonomic character. The present paper describes the structure of the frontal filament and attempts to explain its function in Tracheliastes maculatus copepodids.

MATERIAL AND METHODS

The observations presented here were made when studying the life cycle of T. maculatus (Piasecki unpublished). Eggs in egg sacs were incubated in water-filled crystallizers.

EXPERIMENTS

The newly hatched nauplii metamorphosed into copepodids within 30 minutes. All copepodids kept in Petri dishes died within three days; many of them failed even to survive the first 24 hours. Some larvae died after extruding their filaments and attaching themselves to the bottom of the dish. When a bream scale was placed in the dish (adult females live attached to bream scales), some copepodids attached themselves to it but never molted further and died. Some copepodids died after only a partial extrusion of the filament (Fig. 4), while others never started the process. Many dead copepodids showed broken cuticle with their hemolymph drained. It was most common in those copepodids which did not extrude their filaments at all or which did so only partially. The mode of filament extrusion was reconstructed from dead copepodids ending their life in different stages of the process. It was only

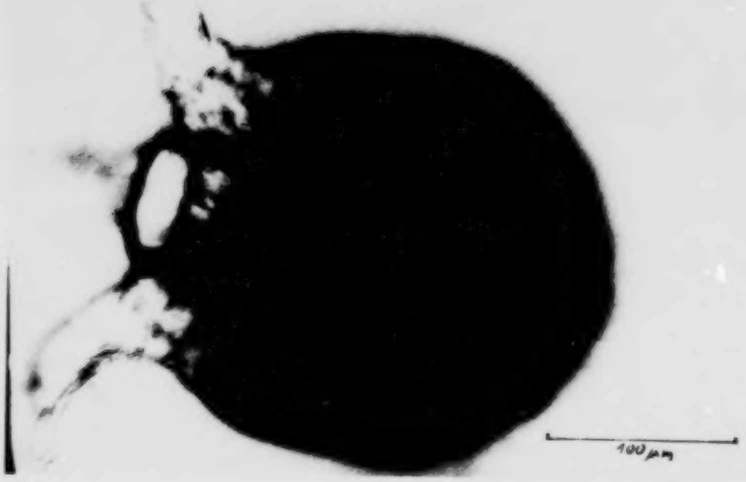

Figure 1: *A free-swimming nauplius. The filament is already fully developed.*

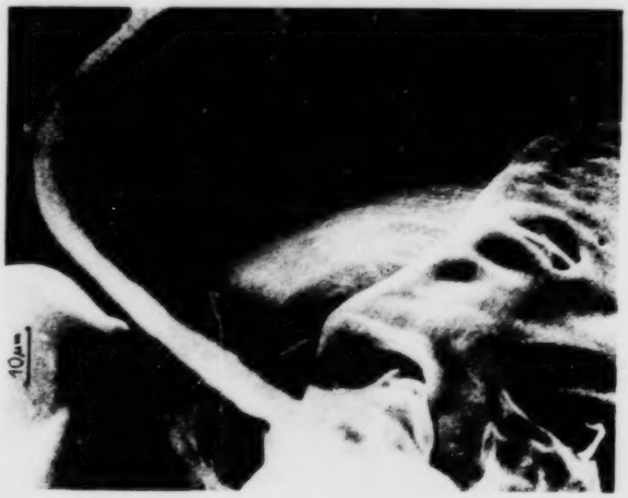

Figure 2: *The anterior part of the cephalothorax, with the terminal plug inserted similar to a bullet in its shell.*

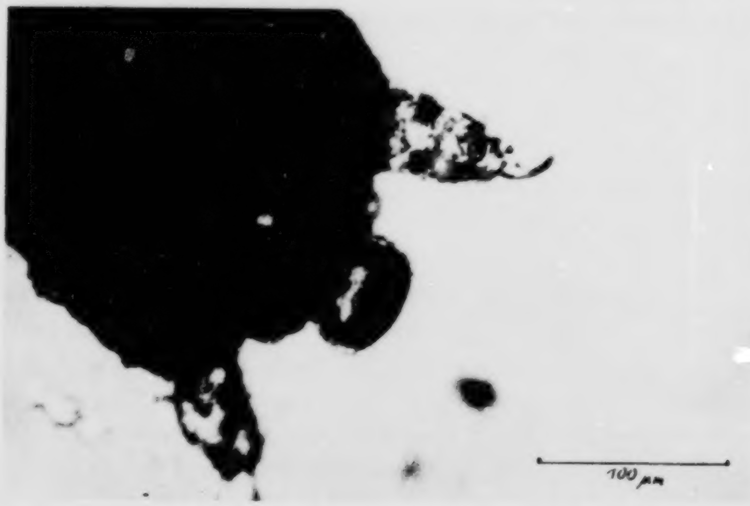

Figure 3: *Phase 1 of the filament extrusion. Dorsal view of anterior part of copepodid.*

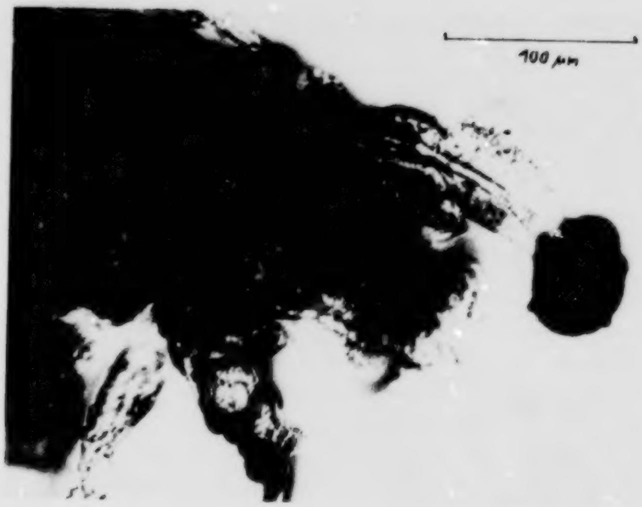

Figure 4: *intermediate phase. Lateral view of copepodid. The plug is followed by the distal section of the filament in a thick aveola. Filament coils are visible inside the cephalothorax.*

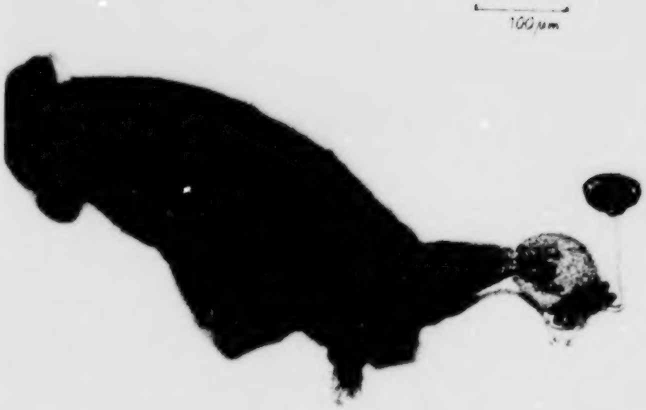

Figure 5: *Terminal phase. The everted filament case drives the coils out, erects the proximal section of the filament, and makes the basal plug to turn by 180°.*

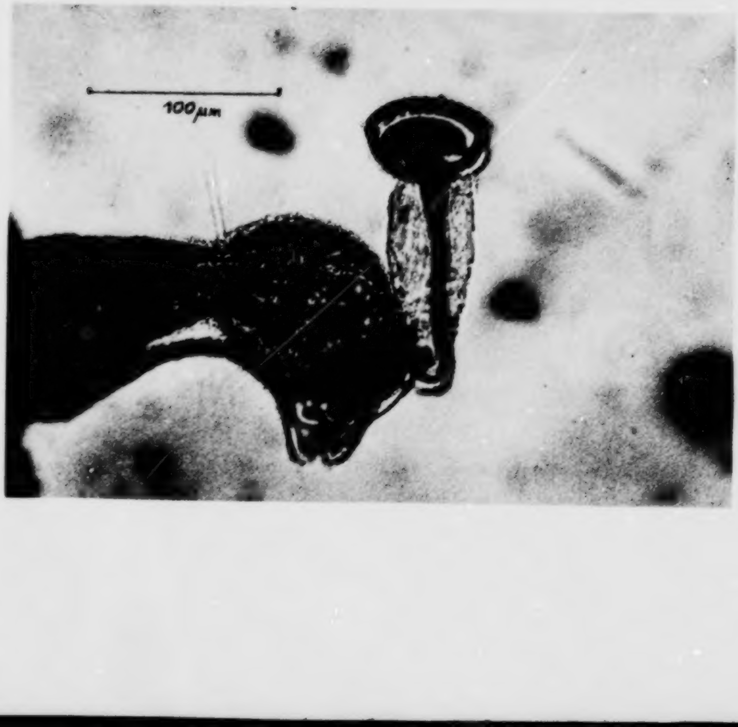

Figure 6. *Enlargement of Fig. 5.*

phase 1, as performed by a life copepodid, that could be observed under a microscope.

FILAMENT AND ITS EXTRUSION

The frontal filament appears very early in the life history of T. maculatus. The terminal plug of the organ is visible soon after pigment spots appear in the eggs. The hatched nauplii show the filament to be already developed (Fig 1). The frontal filament is functional in the next developmental stage, the copepodid. When fully developed this organ consists of a very large terminal plug, a middle coiled filament, and a small basal plug. The terminal plug is more or less spherical, flattened or cut off at its poles. The attachment pole is more flattened than the opposite one. The plug diameter is measured on its equatorial plane is 60 - 70 um. SEM examinations (Fig. 2) revealed the plug to be located in a pit in the anterior cephalothoracic margin. The terminal plug and the distal section of the filament are covered by a layer of gelatinous substance and protected by a thin membrane. The filament is 7 - 10 um in diameter. Its distal part is straight and begins to coil at about 140 um from the terminal plug. The coils are located in the mid-cephalothorax at the level of eye pigment. The proximal section of the filament is straigth, running from the coils to the anterior marigin of the cephalothorax and terminating with the basal plug. This plug is much smaller than the terminal plug and tapers toward its end. Its side is firmly attached to the filament case near the anterior margin of the cephalothorax. The elements described above are usually hidden in the filament case, with only the anterior part of the terminal plug protruding (Fig. 7A). Above this plug, two pairs of sensory setules are seen on the dorsal side of the copepodid. Presumably they play a role in examining the substrate the filament is to be attached to. A similar function may be performed by the mouth apparatus.

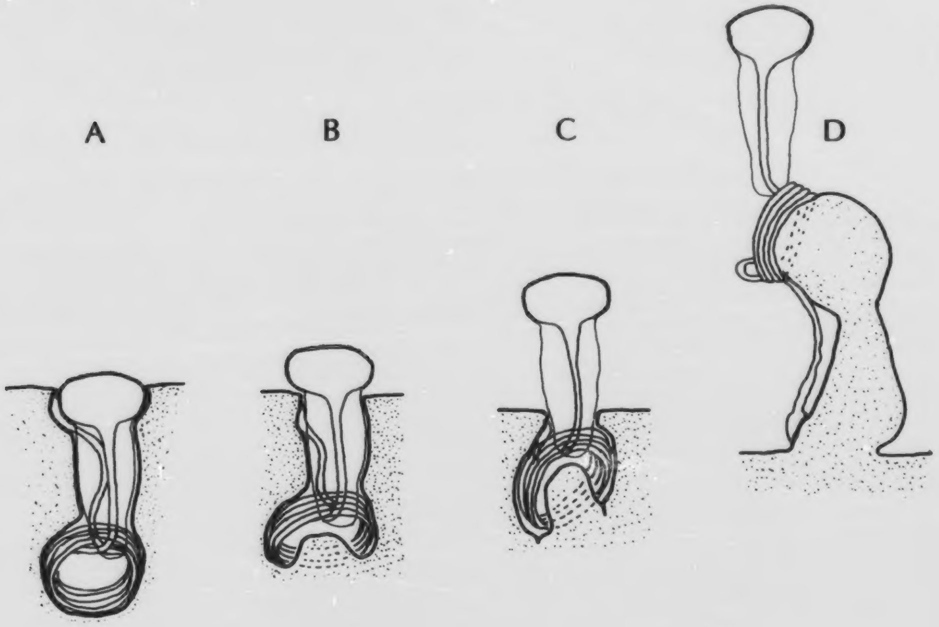

Figure 7: *A diagram of the phases of the filament extrusion: A. The initial position of the filament. B. Phase 1. C. Intermediate phase. D. Terminal phase.*

At the inital phase of the extrusion of the filament (Fig. 3 and Fig. 7B), the plug and the filament in its thick areola are observed to leave the case. As soon as the entire distal section of the filament is extruded, the filament coils are pushed out by everting the filament case as an inflated rubber glove finger. When everting, the case pulls with itself and errects the proximal section of the filament. The coils, previously at the bottom of the case, are now at the top of the extruded "inflated finger" (Figures 5, 6 and 7 D) The basal plug is turned by 180°. The extrusion mechanism of the filament is of a hydraulic nature. The extrusion is caused by increasing internal pressure within the body, as confirmed by dead copepodids which failed to withstand the increased pressure.

According to Kabata and Cousens (1973), the plug attaches itself by means of a cement substance produced by an undefined frontal gland. The gelatinous substance surrounding the terminal plug and the distal part of the filament is likely to play the cementing rôle as it was not observed in those copepodids which had attached themselves to a fish scale. Both the plug and the filament seem to contain no other cementing substance inside as they are the firmest parts of the copepodid body, they remain unchanged on body deterioration or after crushing the body with a coverslip.

In the lernaeopodid chalimus larvae, the plug is attached to the top of the second maxilla. In the present study, a single copepodid was observed with the plug at the top of the second antenna. Presumably, the appendage transfers the filament from the anterior margin of the cephalothorax to the second maxilla.

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SOME USUALLY OVERLOOKED CRYPTIC COPEPOD HABITATS

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Abstract: Many species of free-living cyclopoid and harpacticoid copepods occur in groundwater and cryptic microcosmic and semiterrestrial habitats, such as phytotelmata, small temporary containers, terrestrial and arboreal mosses, bogs and marshes, moist soils, leaf litter, compost heaps and dead wood. Survey collections have often ignored these habitats. Collecting from these habitats using a variety of methods is recommended.

This article reviews some commonly overlooked habitats of cyclopoid and harpacticoid copepods, in the hope of stimulating more collecting from them. Though it was recognized early that a variety of freshwater and semiterrestrial habitats, some only intermittently moist, may support free-living cyclopoid and harpacticoid copepods (Chappuis 1917, Menzel 1926, Mrázek 1893), collectors on many expeditions have sampled primarily from openwater lacustrine, riverine and sometimes subterranean locales. The efficiency of collectors in terms of the proportion of previously unknown species found generally rises in proportion to the effort expended in sampling more cryptic habitats (Table 1).

Table 1. *Number of locales according to type of habitat sampled during some general collections, and numbers of copepod species encountered. *indicates group not included in survey.*

Reference	Lakes, plankton	Lakes, littoral	Lakes, benthos	Pools and ditches	Rivers, plankton	Rivers, littoral	Streams and waterfalls	Marshes and bogs	Springs	Caves	Wells	Groundwater and psammon	Phytotelmata	Soil and leaf litter	Calanoid species	Cyclopoid species	Harpacticoid species	New species	% new species found
Dussart (1982)	12	4	-	16	-	-	2	-	4	2	-	3	1	-	3	28	10	4	10
Harding (1955)	27	7	-	8	-	3	5	2	2	-	-	-	-	-	7	15	7	7	24
Kiefer (1934)	56	2	-	11	7	-	3	-	-	-	-	-	-	-	15	20	3	1	2
Kiefer (1952)	9	4	-	3	4	1	-	-	-	-	-	-	-	-	2	42	*	15	34
Lowndes (1930)	11	-	-	3	-	-	-	-	-	-	-	-	-	-	2	13	1	1	6
Lowndes(1934)	1	1	-	13	2	-	-	4	-	-	2	-	-	-	6	14	1	9	43
Noodt (1965)	-	-	-	-	-	-	-	-	-	-	-	7	-	-	*	*	13	13	100
Plesa (1981)	2	-	-	2	-	-	-	-	-	20	4	3	-	-	*	22	*	6	27
Reid (in press)	-	-	-	-	-	-	-	1	1	-	-	-	-	1	0	4	29	32	90
Rouch (1962)	-	1	3	-	-	-	1	-	-	-	-	3	-	1	*	*	9	6	66
Smith and Fernando (1978)	206	-	-	-	-	-	-	-	-	-	-	-	-	-	4	22	*	0	0

These habitats fall into three categories: (1) aquatic microcosms, in which a small volume of water has collected, either temporarily or semipermanently; (2) semiterrestrial habitats, a loose grouping of intermittently or permanently moist habitats with no obvious open water present; and (3) man-made habitats. There may or may not exist any physical continuity with nearby groundwater or open-water systems.

(1) Aquatic microcosms have long served as convenient collecting sites of aquatic fauna (Müller, 1879). Phytotelmata or containers formed by living plants such as bromeliads, pitcher plants, and leaf axils have yielded members of the harpacticoid genera *Attheyella*, *Elaphoidella*, *Epactophanes*, *Antarctobiotus* and *Phyllognathopus*, and the cyclopoid genera *Paracyclops*, *Tropocyclops*, *Ectocyclops*, *Bryocyclops* and *Muscocyclops* (Chappuis, 1936; Dussart, 1982; Kiefer, 1929; Lang, 1948; Scourfield, 1939 and V.F. Hadel, personal communication). *Cryptocyclops anninae* was first collected from the water contained in empty coconut husks (Lowndes, 1928), and *Tropocyclops schubarti dispar* was found in the shells of fallen Brazil nuts (Herbst, 1962). Maguire (1971) reported copepods in the water cupped in fallen leaves on the floor of a Puerto Rican rain forest. Tiny pools in rock hollows yielded two species of cyclopoids (Scourfield, 1939). Gurney (1920) and Scourfield (1915, 1939) reported two species of *Moraria* from water or even the "earthy deposit" in treeholes in England. *Mesocyclops aspericornis* has been collected from crab burrows in Polynesian atolls (B. H. Dussart, personal communication).

(2) Aquatic species may form an important component of the cryptozoic fauna of the forest floor, as first recognized by Dendy (1895). Copepods are frequently recorded from moist soils or leaf litter. Reid (1982, in press) isolated 4 species of cyclopoids and 29 species of harpacticoids from the moist organic soil of a neotropical wet campo marsh; 18 species persisted in the thin layer of organic topsoil at the uphill margin of the marsh, at total densities of 1000 to 178.000 individuals m^{-2}. In the soil of a sedge meadow in the Canadian tundra, mean densities of 6541 copepods m^{-2} were recorded by wet and dry funnel extractions (Bliss et al., 1973). Sturm (1978), using direct counts, found up to 3000 individuals m^{-2} of the harpacticoids *Epactophanes richardi* and *Elaphoidella* sp. in the moist soils of the Páramo region in the Columbian Andes. Sturm also recovered these species in Barber traps (Barber 1931), but not by the Berlese-Tullgren funnel method. The exclusive use of the latter method may explain why copepods are not mentioned in some careful studies of soil fauna (Lawrence, 1953) or barely included in reviews, even if bog, fen and other wetland soils are considered (Wallwork, 1976). Plowman (1979) did list copepods as well as ostracods and amphipods from litter in a wet sclerophyll forest in Australia. Wallwork (1976) mentioned that in moist beech litter in southern England, harpacticoids are "surprisingly abundant"; Scourfield (1939) listed six species of harpacticoids recovered from leaf litter in England. When beech forest litter in New Zealand was placed in petri dishes containing water, a cyclopoid (*Gonicyclops silvestris*) and a harpacticoid (*Bryocamptus stouti*) were found swimming in the cultures (Harding, 1958). Damp leaves in both a 25-year-old and a 6-month-old compost heap in Maryland, U.S.A., harbor large populations of *Phyllognathopus viguieri* (T.E. Bowman, personal communication, and Reid, unpublished data). *Phyllognathopus camptoides* was described by Bozić (1965) from dead wood collected on the forest floor near a pond in Gabon. Copepods have also been collected from ants' nests (B.H. Dussart, personal communication).

Sphagnum bogs and terrestrial mosses in both temperate and tropical regions have yielded many species of the harpacticoid families Phyllognathopodidae, Canthocamptidae and Parastenocarididae and the cyclopoid genera *Bryocyclops*, *Ectocyclops*, *Menzeliella* and *Muscocyclops* (Chappuis, 1917, 1936; Herbst, 1959; Menzel, 1926; Scourfield, 1939). Maguire (1971) encountered copepods as well as numerous other aquatic animals in squeezings from wet arboreal hanging mosses in a Puerto Rican rain forest.

(3) Man-made habitats harboring copepods have included water tanks (Chappuis, 1936; Scourfield, 1939), the filtration apparatus of a municipal water treatment plant (Kunz, 1976), and the saucer of a

flowerpot (Kiefer, 1960).

Thus copepods may inhabit facultatively many aquatic and semiterrestrial habitats usually neglected by collectors. Many species described from such habitats are known from only one or a few records. In this connection Kiefer (1952) observed that "vor allem sind extreme Biotope wie Grundwasser, Klein- und Kleinstgewässer aller Art (z.B. nasse Moose, Phytotelmen usw.) bislang erst ganz ungenügend auf Copepoden hin untersucht worden." Imaginative collecting from all possible habitats using a variety of methods should be included in any survey, even though this necessitates laborious extraction and sorting procedures. Since copepods may be attracted to localized food sources (Hicks and Coull, 1983), investigation of the efficiency of baited traps such as the Barber type may be worthwhile.

ACKNOWLEDGEMENTS

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BIBLIOGRAPHY OF CANADIAN AQUATIC INVERTEBRATES WITH AN EXAMPLE FROM COPEPODA

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In 1973 the now defunct Canadian Oceanographic Identification Centre started a bibliographic project to compile a list of invertebrates recorded from aquatic environments in Canada. This project was subsequently carried on and expanded by Invertebrate Zoology Division of the National Museum of Natural Sciences when the Centre was amalgamated with the Division. It was computerized in 1981 when the National Inventory Programme (now the Canadian Heritage Information Network) of the National Museums of Canada incorporated the data into the Museums' computer system.

The primary objective of our project, Bibiliography of Canadian Aquatic Invertebrates, is to assemble from the scientific literature the information on all aspects of research on aquatic invertebrates (protozoans, insects, and endoparasites excluded) of the marine and fresh waters of Canada and the contiguous area, including Alaska and the Aleutian Islands, Puget Sound, Lake Champlain, and the Great Lakes with the exception of Lake Michigan. In this paper we shall briefly describe our project from literature search to applications of the computerized data (Fig. 1).

LITERATURE SEARCH

We used conventional tools, such as Zoological Record and Biological Abstracts, and complete runs of more than forty scientific journals that have been the primary sources for publications on aquatic invertebrates in general and Canadian fauna in particular as the foundation for our search of the literature. A publication was included in our file if it reported some aspect of at least one invertebrate with a scientific name of generic level or lower and with an indication of the source of occurrence of this animal within the geographic area of our study (a mere mention of Canada was not accepted). We also checked the references cited in the publications reviewed. As a result we have accumulated nearly 5,000 articles published prior to 1977 in our bibliographic file (Sharma et al., 1983). Recent publications are available from several commercial computerized retrieval systems and were, therefore, not included in our original basic search.

ABSTRACT OF INFORMATION

When a publication is to be included in our file, its information is recorded on two cards for later transfer to the computer system.

An Author Card with the information of the author(s), publication date, title, and source of citation is prepared. The source of citation is abbreviated according to the format used by BIOSIS. A Reference Number is assigned for each publication. An article by Wailes is used here as an example:

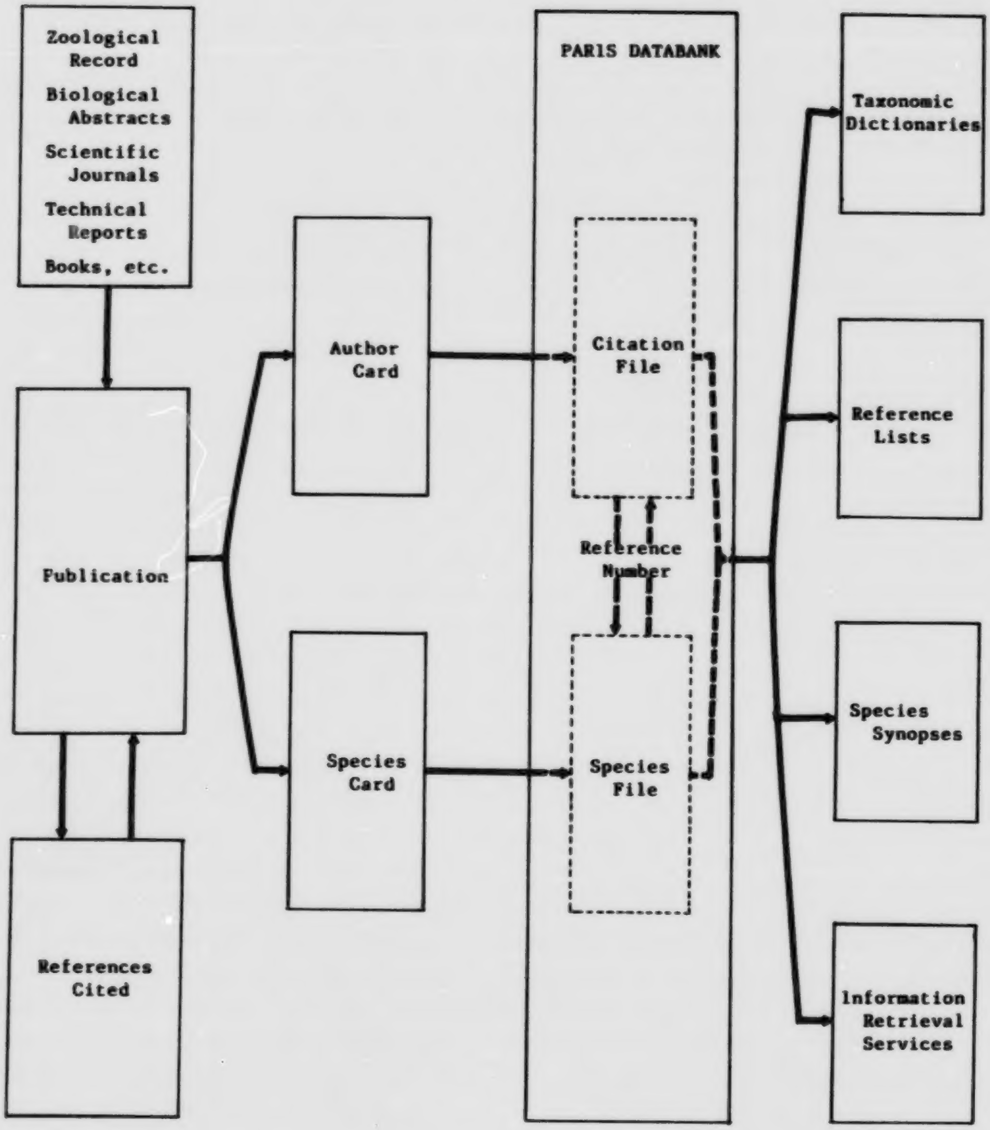
Zoological Record
Biological Abstracts
Scientific Journals
Technical Reports
Books, etc.
Publication
References Cited
Author Card
Species Card
PARIS DATABANK
Citation File
Reference Number
Species File
Taxonomic Dictionaries
Reference Lists
Species Synopses
Information Retrieval Services

Figure 1. *Procedures and applications of the project, Bibliography of Canadian Aquatic Invertebrates.*

Wailes, G.H. 1929. 4728
The marine zooplankton of British Columbia.
Vancouver Mus., Mus. Art Notes, 5:30-32.

The number, 4728, on the upper right corner of the card is the Reference Number for this article.

The information on the scientific name (at generic level or lower), general habitat, locality, and subjects of study of each animal is entered on an Abstract Card. Here is an example for the same article:

4728 Wailes, G.H. 1929.
Marine
Pacific

Acartia clausi	Distribution
Acartia longiremis	Distribution; Ecology
Anamolocera pattersoni	Distribution; Ecology

(The rest of the record of this article is omitted)

We have enlisted 16 keywords to describe the subjects of study and divided our studied area into three marine regions (Atlantic, Arctic, and Pacific) and 15 freshwater regions (ten provinces and two territories of Canada, Alaska, Great Lakes, and Lake Champlain).

Before entering the records to our database, we check the spelling, authority and date, current acceptability, and higher taxonomic hierarchy (family and higher levels) of each scientific name. We accept the scientific identity reported by the author unless that identity has been corrected later in the literature. In the above example the correct spelling of *Anamolocera pattersoni* is *Anomalocera patersoni* which was described by Templeton in 1837. The records of this species from the eastern North Pacific, according to several authors in the literature, are misidentifications of *Epilabidocera longipedata* (Sato, 1913).

COMPUTER DATABASE

Our computerized data are stored in the Paris system (Pictorial and Artifact Retrieval and Information System) at the Canadian Heritage Information Network. There are two files: citation and species. The two files are linked by the Reference Number of a publication. The citation file contains the information on the Author Cards. Each scientific name and its accompanying information reported in a publication and recorded on our Abstract Card constitutes a document in the species file. The above example of the record of *Anamolocera pattersoni* in Wailes (1929) is shown here:

PARIS NUMBER	97682
PREVIOUS NUMBER	67284
AQUISITION NUMBER	4728
SYNONYMS	ANOMALOCERA PATERSONI TEMPLETON 1837
FORMER GENUS	ANAMOLOCERA PATTERSONI
GENUS	EPILABIDOCERA
SPECIES	LONGIPEDATA
SPECIES AUTHORITY	(SATO
SPECIES DATE	1913)
FAMILY	PONTELLIDAE
PHYLUM	CRUSTACEA
CLASS	COPEPODA
ORDER	CALANOIDA
ECOLOGY/GEN.HABITAT	MARINE
ORIGIN-OCEAN/BASIN	ATLANTIC
ORIGIN-PROVINCE/TERR.	
TOPIC OF PUBLICATION	DISTRIBUTION; ECOLOGY
AUTHOR	WAILES, G.H.
DATE OF PUBLICATION	1929.

The first three fields are numbers used for various internal purposes, e.g., AQUISITION NUMBER is for our Reference Number. If the scientific name reported in the article is currently considered as a synonym of another name, it will be entered in SYNONYMS and the latter will be entered in the four fields: GENUS, SPECIES, SPECIES AUTHORITY, and SPECIES DATE. If the reported name is a valid name, it will be entered in both SYNONYMS and the other four fields. If the scientific name is misspelled in the publication, the misspelled name will be entered in the field FORMER GENUS. (Because we are using a system designed for collection data, we have had to adapt to the already established fields. In this case, FORMER GENUS was closest to our requirement for a field to cover authors' or other lapses.) Names of the higher taxonomic hierarchy of a scientific name are entered in the next four fields: FAMILY, PHYLUM, CLASS, and ORDER.

ECOLOGY/GEN. HABITAT is a field for the general habitat of the taxon, e.g., marine, freshwater, saline lake etc. ORIGIN-OCEAN/BASIN is for marine geographic regions and ORIGIN-PROVINCE/TERR. for freshwater regions.

TOPIC OF PUBLICATION is a field for the subjects of study of the publication using whatever selection of the 16 keywords is relevant to the particular species in that publication.

The last two fields are for the author(s) and date of the publication. If there are two authors, the initials of the second author will not be entered e.g., WAILES, G.H., CLEMENS. If there are three or more authors, only the first author's family name and initials followed by et al. will be entered, e.g., WAILES, G.H. ET AL.

APPLICATIONS OF THE COMPUTERIZED DATA

With the computerization of our bibliographic file we have started a new series of publications: Bibliographia Invertebratorum Aquaticorum Canadensium, or Bibliographia. Three kinds of publications are being produced:

Taxonomic dictionary. We have published a list of generic names applied to the aquatic invertebrates of our studied area (Laubitz, et al., 1983). Other faunistic dictionaries can be compiled as required.

Reference list. We have published a list of the references used by our project (Sharma, et al., 1983). Other reference lists for different purposes can also be retrieved, e.g., by major taxonomic group.

Synoptic information of a taxonomic group. We intend to publish a series of species synopses of different taxonomic groups under the general heading of *Synopsis Speciorum*. The original individual entries for each species will be reorganized and combined, so that the families within a taxon are arranged alphabetically as are the genera and species within each family. The information from the literature, on distribution and keyword topics, is listed chronologically by author. Three issues have been published (Chengalath, 1984; Madill, 1985; Rafi, 1985) and several are in preparation, including one on Copepoda by CtS and IS. All volumes of *Synopsis Speciorum* are updated to include the literature from 1977 to the date of their completion.

We can also provide retrieval services to persons requiring information on any aquatic invertebrates of our studied area. For example we may compile a species list of particular taxonomic groups recorded in a geographic region within our area.

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Sharma, N., D.R. Laubitz, I. Sutherland, P. Adams, and C.-t. Shih. 1983. Index Bibliographicus. Bibliographia Invertebratorum Aquaticorum Canadensium. Volume 2. National Museums of Canada, Ottawa: 240p.

EFFECT OF INCUBATION TIME AND CONCENTRATION OF ANIMALS IN GRAZING EXPERIMENTS USING A NARROW SIZE RANGE OF PARTICLES

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Abstract: Three concentrations of A. tonsa adults were allowed to feed on a narrow size range suspension of particles. Sampling was done at 4-hour intervals during 24 hours. It is shown that both animal concentration and incubation time considerably influence the obtained ingestion rates and filtering-spectra. These results are discussed in relation to different calculation methods and models.

INTRODUCTION

The particle counting method (Fuller and Clarke, 1936) is the most common technique, apart from the use of radio-tracers, for grazing measurements. It is used mainly in studies which focus on selectivity of grazing. Using this technique, an experiment is set up to create a difference in particle concentration which is detectable by microscopical or electronical counting. The ingestion rates calculated from this decrease, expressed in biomass per animal per unit of time, are a reliable estimation of the animal's feeding activity in natural circumstances only if the results obtained are independent of the concentration of animals and the incubation time used for the experiment. Several authors have demonstrated that both these factors can influence the measured feeding activity: Anraku (1964), Richman et al. (1977, 1980), Roman and Rublee (1980).

Alerted by these results, we have reinvestigated the combined effect of concentration of animals and incubation time on the grazing of the calanoid copepod Acartia tonsa. This paper reports the results of two experiments performed with a narrow range of particles as food suspension.

MATERIAL AND METHODS

A non-sterile culture of Chlamydomonas sp. which also contained small coccoid cells was used as food. Counting was done with a Coulter counter model TA II equiped with a 100 µm aperture tube. In the analysis a particle size spectrum of 8 size classes, with a spheric equivalent diameter ranging from 1.80 to 9.09 µm was considered. Total initial particle concentration was 60,000 particles ml^{-1} in experiment 1 and 98,500 particles ml^{-1} in experiment 2 (Fig. 1). Expressed in volume the peak caused by the small coccoid cells (class 1) is much less important than the Chlamydomonas peak (class 5).

Acartia tonsa adults were collected from a large out door culture tank. Immediately after capture, the animals were sorted into groups of five in petri-dishes containing 10 ml of the algal suspension to

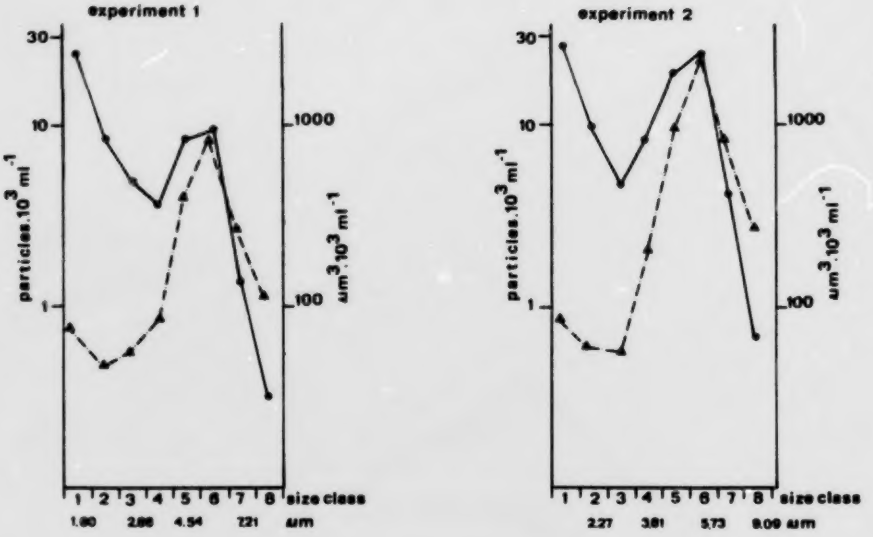

Figure 1. *Experiments 1 and 2: Initial particle concentration in numbers (left scale, •—•) and in volume (right scale, ▲---▲). In absissa: size classes with spheric equivalent diameter.*

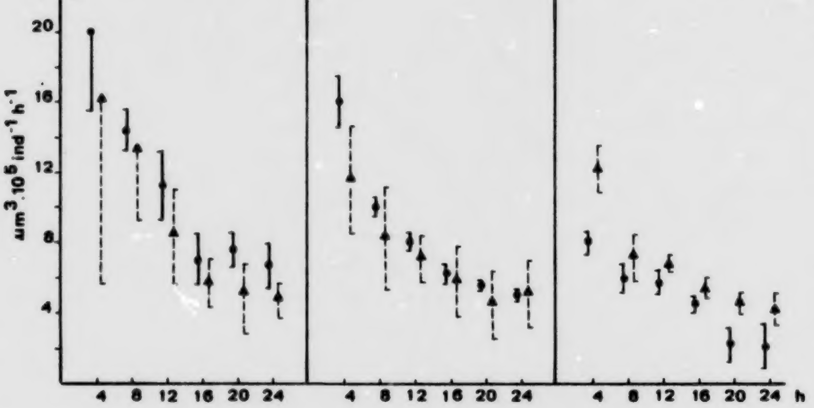

Figure 2. *Total ingestion rate (I) vs incubation time. • : experiment 1; ▲ : experiment 2. a) 25 Acartia l^{-1}; b) 50 Acartia l^{-1}; c) 100 Acartia l^{-1} standard deviation indicated by vertical bars.*

be used in the experiment. Each experiment consisted of 3 series: a) 25, b) 50 and c) 100 animals liter^{-1}. At the beginning of the experiment, four 1 liter bottles were filled with algal suspension to serve as controls. The grazing bottles were first filled with 250 ml of algal suspension. The appropriate number of dishes containing 5 animals were gently poured into each bottle. Care was taken to distribute animals that had been isolated at the beginning and at the end of the isolation procedure equally over the 12 grazing bottles so that each bottle contained a mixture of animals that had been preincubated on the experimental algal suspension for a period between 1/4 and 2 hours. The grazing bottles were then filled with algal suspension up to a volume of 1 liter. The bottles were rotated at 2 rpm in the dark at room temperature. This was between 18^{o} and 22^{o}C for both experiments, the maximal variation during one experiment being two degrees. Total incubation time was 24 hours. Every 4 hours, a 60 ml sample was taken from each bottle with a pipette covered with a 50 μm net to avoid catching the animals. These samples were returned to the bottles after counting.

For each size class, filtering rates (F) and ingestion rates (I) were calculated following Frost (1972), using the mean of the 4 control bottles as control value. F was counted as 0 if particle concentration in the grazing bottle was higher than the control value. Ingestion rates were calculated as volumes by multiplying the number of particles ingested by the spheric equivalent volume.

The results obtained after each sampling are indicated as, for example, (25,4), i.e., 25 animals incubated for 4 hours.

RESULTS

Total ingestion rate (I) is plotted against incubation time for the 3 series in Fig. 2. In both experiments, I declines significantly with time (Von Neumann test, $p < 0.05$). A decline in I with concentration of animals is also observable, but could not be tested statistically because of insufficient data. Coefficients of variation between the four replicate I values show no significant trend with time (Spearman's rank-correlation test, $p > 0.05$).

Fig. 3 shows the filtration patterns (i.e. filtering rate for each size class) obtained in the 3 series after each sampling of experiments. Mean F-values marked by a cross indicate that at least one of the experimental bottles showed a higher particle concentration after incubation than the control value. In (25,4) both the largest and the smallest size classes have high F-values, while the ones forming the volume peak have lower F-values. In contrast, the pattern in (100,24) shows lower F-values for the smallest size classes than for the ones forming the volume peak and the largest ones. The type of pattern of (25,4) persist through all incubation times in series (25,t). It also occurs, (although less pronounced) for short incubation times in series (50,t). It is never observed in series (100,t). The change in F-values is most pronounced in the smallest size classes: the high filtering rates measured with low animal concentrations and short incubation completely disappear when high animal concentrations or long incubation times are used.

The filtration pattern in experiment 2 shows that same trend (Fig. 4). Filtering rates are lower than in experiment 1, because of the higher particle concentration. Particle concentration in grazing bottles more frequently exceeds the control value than in experiment 1.

Coefficients of variation between the four replicate filtering rates were calculated for each size class. The coefficients of variation show no significant trend with time in 44 of the 48 cases. (Spearman's rank-correlation test, $p > 0.05$).

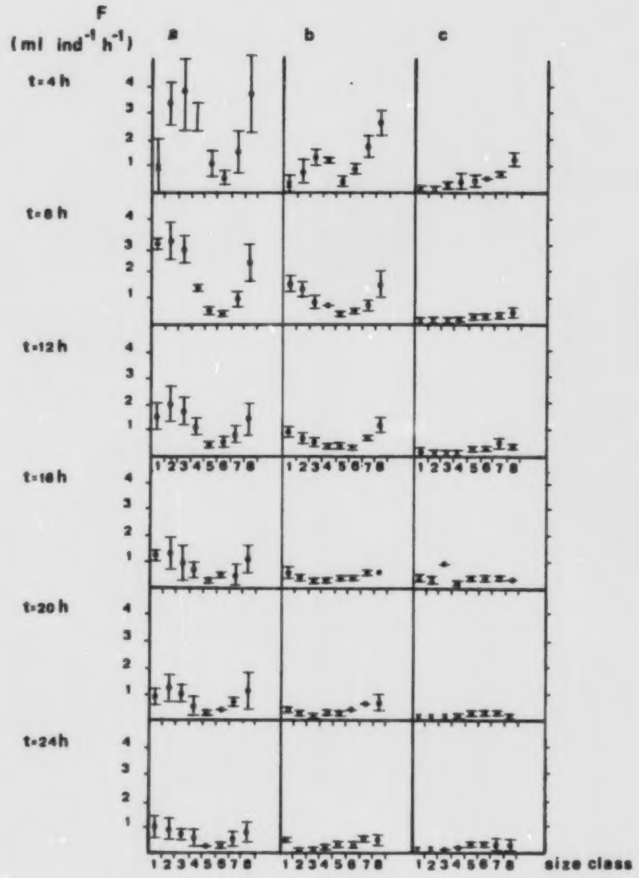

Figure 3: *Experiment 1: Filtration pattern. Filtering rate (F) for all size classes vs incubation time and animal concentration. a): b); c) as in Fig. 2*

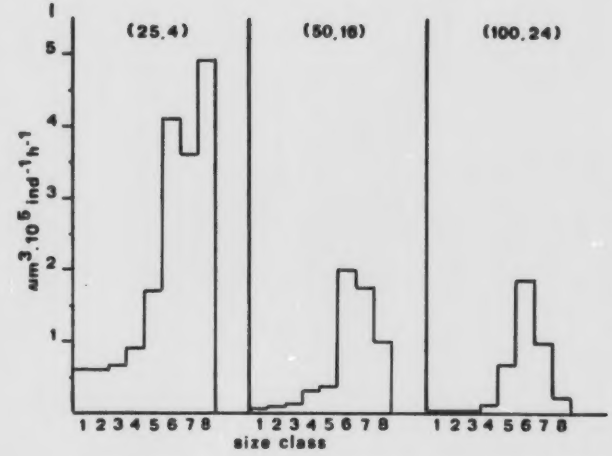

Figure 4: *Experiment 2: Filtration pattern for (25,4), (50,16) and (100,24). See Fig. 3 and text for further explanation.*

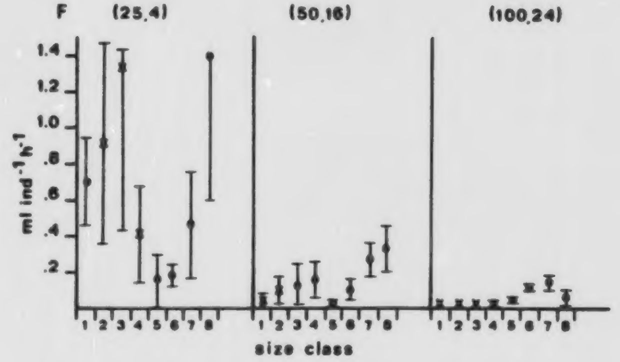

Figure 5: *Total ingestion rate (I), calculated as $I = (C_t - C_{zt}) \frac{V}{Nt}$ • vs incubation time.*
● : experiment 1; ▲ : experiment 2. a), b), c), as in Fig. 2. See text for further explanation.

DISCUSSION

Within the particle size range of 2 to 9 µm covered by the Chlamydomonas-coccoid cell mixture used as food, we find that the results are influenced by incubation time in the same way as reported by Roman and Rublee (1980), working with natural seawater with a particle size range of 2 to 32 µm. In our experiments, increased concentration of animals has the same effect as prolonged incubation.

Williams (1982) has demonstrated that filtering rates can appear to decrease when the animal's filtration efficiency for the food is less then 100%.

As a control on our data, we have avoided the use of filtering rates by calculating ingestion rates as $I = (C_t - C_{zt}) \cdot \frac{V}{Nt}$, where C_t and C_{zt} are the concentrations of particles in a given size class at the end of the incubation period (t) in control and grazing bottles respectively, N the number of animals in the grazing bottles and V the volume of algal suspension in the grazing- and control bottles (ml). The obtained ingestion rates also decline with incubation time and animal concentration (Fig. 5). As ingestion rates are similar in both experiments, it is unlikely that depletion of edible particles takes place, at least in experiment 2 (highest particle concentration). So other factors must be responsible for the decline in ingestion rate.

As demonstrated by Roman and Rublee (1980), one of these factors is the stimulated production of particles in the grazing bottles. In our experiments, this phenomenon becomes visible in the smallest size classes, suggesting growth of the coccoid cells. The fact that particle concentration in the grazing bottles more frequently exceeds the control value in experiment 2 than 1 can be explained by the higher particle concentration. Since ingestion rates are similar in both experiments, excretion rates of nutrients, and possibly of undigested particles can be considered of similar magnitude. An increase of the exponential growth rate caused by increased nutrient concentration in the grazing bottles will be the same in both experiments, as the same type of algal suspension is used. However, in experiment 2, the effect of the animal's ingestion on the particle concentration is more rapidly overtaken by this increased growth rate, which is operating on an originally higher concentration then in experiment 1. This difference noticed between the two experiments in itself indicates that there is an indirect influence of the animal's presence on the particle concentration in the grazing bottles.

Our results do not allow us to determine to what extent factors such as hyperactivity, stress or weakening of the animals in the course of the experiment **also** influence the results. Weakening of the animals, calculation errors and particle production can all be minimized by using low concentration of animals and short incubation times. This recommendation is also supported by the fact that reproducibility of the results is not improved by increasing grazing pressure.

ACKNOWLEDGEMENTS

We thank all members of the "Dutch-Belgian discussion group on grazing", especially Drs. C. Bakker and Dr. W.C.M. Klein Breteler for critical comments on the manuscript. Dr. A.G. Vlasblom gave statistical advice, Dr. E.K. Duursma critically read the manuscript and M.J. van Leerdam typed it.

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SPATIAL SEGREGATION OF COPEPODS IN THE ABRA PORT OF BILBAO

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Abstract: The interspecific and intraspecific spatial segregation of copepods was studied in a portuary zone on the Gulf of Biscay during 1981 and 1982. A fine-scale sampling method to obtain zooplankton samples and techniques of multivariate analysis in the treatment of data were used.

The results revealed a predominant vertical segregation of species, correlated with temperature, in the thermally stratified period and a inshore-offshore species gradient in the thermally homogeneous period, when there are no important mixing processes due to wind. In relation to vertical segregation Paracalanus parvus, Acartia clausi and Oithona nana appeared as surface species while Temora longicornis, Oithona helgolandica and Oncaea subtilis were clearly related to depth. Important intraspecific differences appeared between the males of A. clausi and Euterpina acutifrons and the other components of those species. Both showed apparent hyponeustonic distributions.

INTRODUCTION

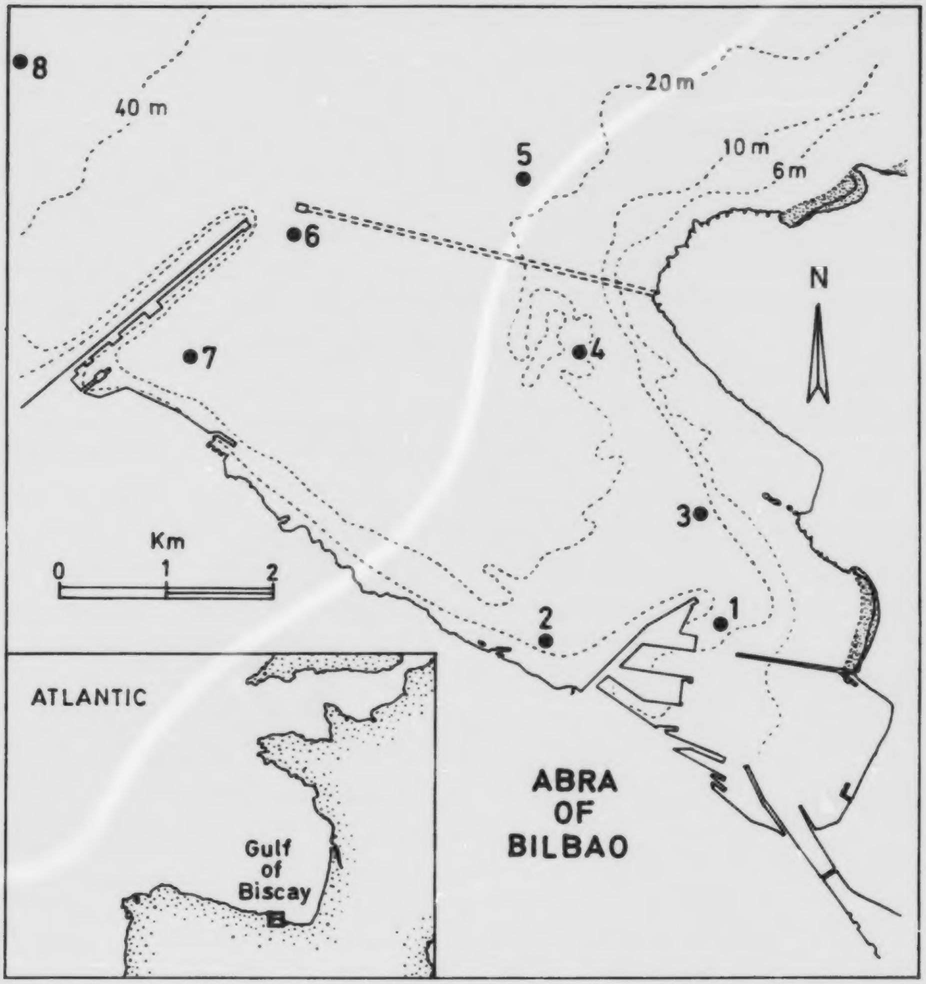
The composition and seasonal variations of copepods in the Gulf of Biscay are well documented by Beaudouin (1975), Vives (1980) and Alvarez-Marqués (1980) in shelf waters, and by Castel (1976), Villate and Orive (1981) and Casamitjana and Urrutia (1982) in coastal estuarine areas. Inshore-offshore and surface-bottom distributions of the species in relation to the physical processes have also been treated in some of the above mentioned papers. However in all of them, samples have been collected by means of plankton nets. This sampling method is suitable in areas of low density of organisms, but there is a lack of information concerning fine-scale spatial distribution of organisms in zones where there are a remarkable spatial gradient of the physical and biological parameters.

The objective of this study is to determine interspecific and intraspecific spatial segregation of copepods in the Abra of Bilbao, a coastal semi-closed area on the Gulf of Biscay, using fine-scale sampling techniques and multivariate analysis.

MATERIALS AND METHODS

Zooplankton samples and hydrological data were collected from May 1981 to May 1982 in the Abra of Bilbao, which is a portuary zone influenced by polluted fresh water effluents and characterized by a semidiurnal tidal cycle. Sampling stations were established according to hydrological and topographical criteria (Fig. 1). Monthly samples were taken at the same tidal phase at three to five depths depending on the bathymetry of each station.

Zooplankton samples were collected by means of 16 litre Van Dorn translucent bottles and filtered through 45 μm nylon netting. This sampling technique allows detection of patchiness, and its advantages


8
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6 m
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3
Km
0
1
2
2
1
ATLANTIC
ABRA
OF
BILBAO
Gulf
of
Biscay

Figure 1. *Study area showing stations sampled.*

in comparison with nets for copepod sampling in eutrophic areas have been described in Alcaraz (1977). Samples were fixed in 80% ethanol.

The identification of copepods included males, females and copepodids; nauplii were not identified. Copepodids of calanoids as well as those of Euterpina acutifrons were divided into three size classes, Oithonidae in two size classes and small species (Oncaeidae and Microsetella norvegica) were lumped as one. Paracalanus parvus, Pseudocalanus elongatus and Clausocalanus sp. copepodids were grouped in a P-calanus taxonomic category. For analysis purposes, P-calanus copepodids have been considered to belong to P. parvus due to the scarcity of P. elongatus and Clausocalanus sp.

The interspecific and intraspecific spatial segregation of copepods has been studied by means of correspondence analysis (CA) which gives a species-samples simultaneous ordination in a reduced space (Legendre et Legendre, 1979). In our case, the study was carried out for the cruises of June, July, August and October 1981 and of March and April 1982, in which there was a maximum abundance of copepods.

RESULTS

CA revealed two different segregation patterns in the Abra of Bilbao: a first group of cruises during the months of June, July and August, in which the greatest proportion of the variance in copepod segregation was related to a vertical gradient, and a second group of cruises (October, March and April) in which the variance did not seem to be related to vertical gradients, and possibly reflected local differences between the different zones of the area studied (Fig. 2). The first group of cruises coincided with a period of thermal stratification (Fig. 3) with a clear dominance of warm water species (P. parvus, Oithona nana, E. acutifrons, Oncaea media and O. subtilis). In June cold water species (A. clausi and Oithona helgolandica) appeared to be well represented too. The second group of cruises was characterized by thermal homogeneity dominated by warm water species in Obtober and by cold water species in March-April.

In June and July, when the water column was thermally stratified but without a clear thermocline, the first CA axis accounted for 39,77% and 38,59% of the variance respectively. In both cruises surface waters (0 m samples) were separated from the rest along this first axis. The males of A. clausi and E. acutifrons in July, and the males of A. clausi in June, contributed almost totally to forming the first axis. Both appeared to be associated with outside surface waters. The second axis accounted for 16,95% of the variance in June and 16,45% in July. In both cruises it seemed to be associated with depth (for samples ranging from 5 m to 20 m) and it was well correlated to the thermal gradient. A vertical trend of the species gradient was evident along this axis in June, when the shallower species was P. parvus, followed by A. clausi and Oithona nana. Oncaea media and Oithona helgolandica showed intermediate depth distributions, while Oncaea subtilis appeared in the deeper levels. In July the trend was not so clear but it maintained a vertical distribution of the species, with Oithona nana and P. parvus as the shallower species and Oncaea subtilis and T. longicornis as the deeper (fig. 4). In June, the third axis (12,40% of the variance) seemed to be associated with local differences inside the Abra, with A. clausi associated with the inshore station 2 and Oncaea media with the offshore station 6. Both stations showed the highest mean salinity in this cruise. In July the third axis explained 12,54% of the variance and separated E. acutifrons (except males) which appeared to be associated with middle-bottom depth samples of station 4 from the rest.

In August there was a thermocline between 10 m and 20 m depth. In this cruise the first CA axis (42,69% of the variance) is related to the thermal gradient. The highest contribution to the variability was due to Oncaea subtilis, Oithona helgolandica and to the samples from below the thermocline. Oncaea media and E. acutifrons did not seem to have a clear position and Oithona nana and P. parvus were situated at the surface. The second axis explained 24,62% of the variance and separated surface (0 m samples) from the rest. The third axis (11,92% of the variance) accounted for local differences between surface samples associated with P. parvus and surface samples associated with E. acutifrons males.

In October the first three CA axes did not explain vertical or inshore-offshore gradients of species distribution. Oncaea subtilis in contrast to small P-calanus and Oithona sp. copepodids were the main contributors to the formation of the first axis (29,02% of the variance). The second axis (18,09% of the variance) separated Oncaea subtilis, O. media and M. norvegica from the rest. The same accounted for P. parvus in the third axis (12,34%). A similar situation appeared in March when the first axis (34,61% of the variance) accounted for the opposition between Oncaea subtilis mainly associated with middle depths at station 6 and P. parvus associated with middle-bottom depths of inshore stations 1, 3 and 4. The second and third axes accounted for 22,79% and 12,20% of the variance and separated A. clausi, associated with sub-surface samples at stations 2 and 7 from the rest.

In April the first CA axis accounted for 41,91% of variance and explained opposition between inshore stations with river influence (stations 1, 3 and 4) and offshore stations with marine influence (stations 2, 5, 6 and 7). Inshore stations appeared associated with P-calanus copepodids and Oncaea subtilis. A. clausi (except males) was related to middle and sub-surface waters in offshore stations. The second axis (15,68% of the variance) separated offshore surface water from the rest and the third axis (9,21% of the variance) separated surface waters associated with E. acutifrons males and surface waters associated with A. clausi males from the rest.

DISCUSSION

Interspecific segregation

The turbulence caused by wind action seems to be a determing factor in the distribution of planktonic organisms in the Abra of Bilbao, wind action initiates horizontal as well as vertical mixing processes that would have as a consequence the homogenization of populations. This would be the case in the October and April cruises that were realized when the sea was turbulent. In none of them has the CA allowed detection of a significant species segregation. However, when water turbulence is nill or slight, surface-bottom and inshore-offshore segregation gradients of species appear. The relative importance of each spatial segregation pattern is related to seasonal changes, which influence the thermal stratification of water. When there is an accentuated temperature gradient (cruises of June and July) or a well established thermocline (August), the highest percentage of variance explains differences in the vertical segregation of species related to the temperature and the depth. In all of them, with few variations, has been observed an ordination of species from surface to bottom that would be: P. parvus and Oithona nana, A. clausi, Oncaea media and Oithona helgolandica and lastly Oncaea subtilis and T. longicornis (Fig. 4). A similar ordination along the surface-bottom marine gradient is showed by Vives (1980) in shelf waters of the Basque coast. In Fiedler (1983) a similar vertical

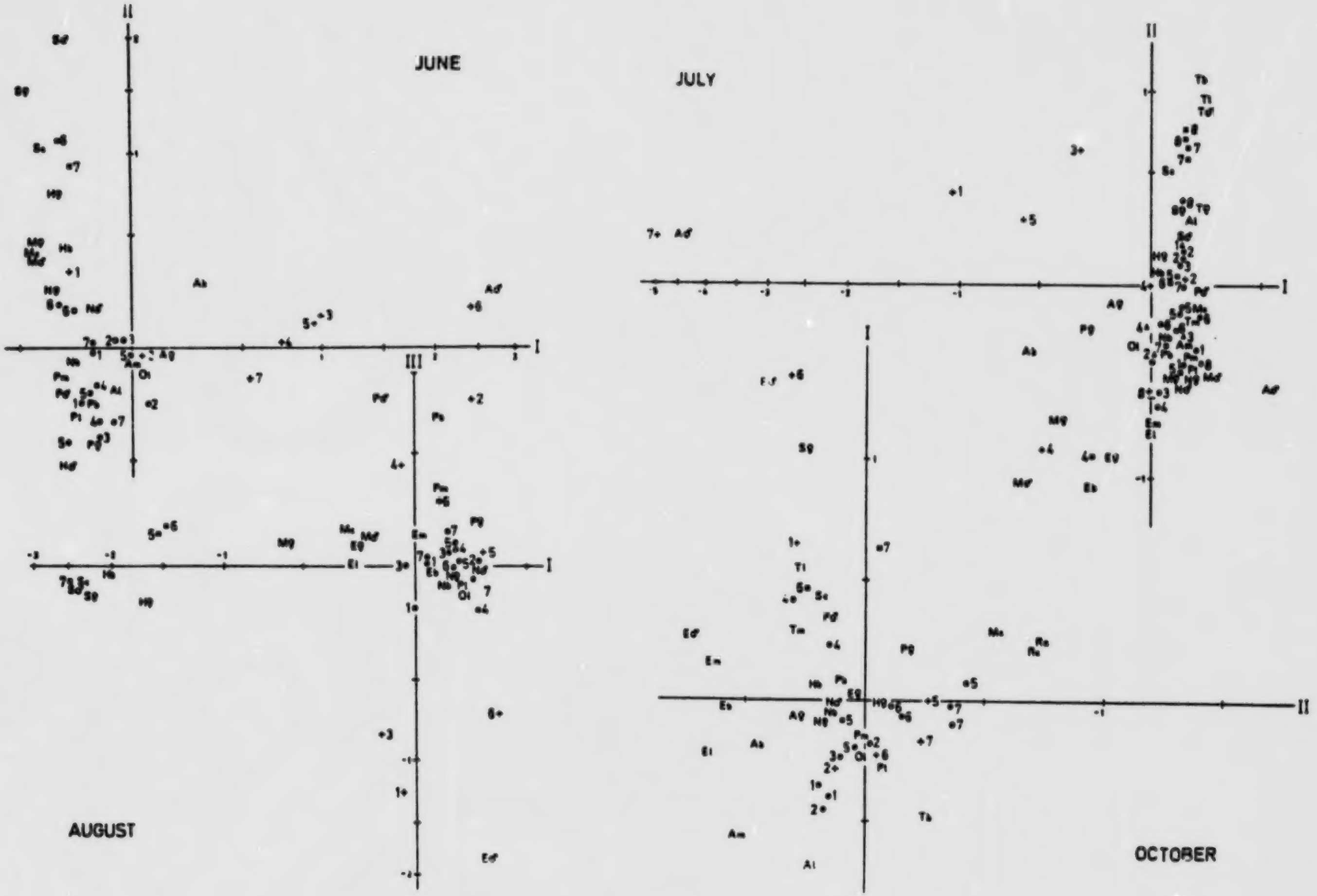

Figure 2. *(See next page for explanation)*

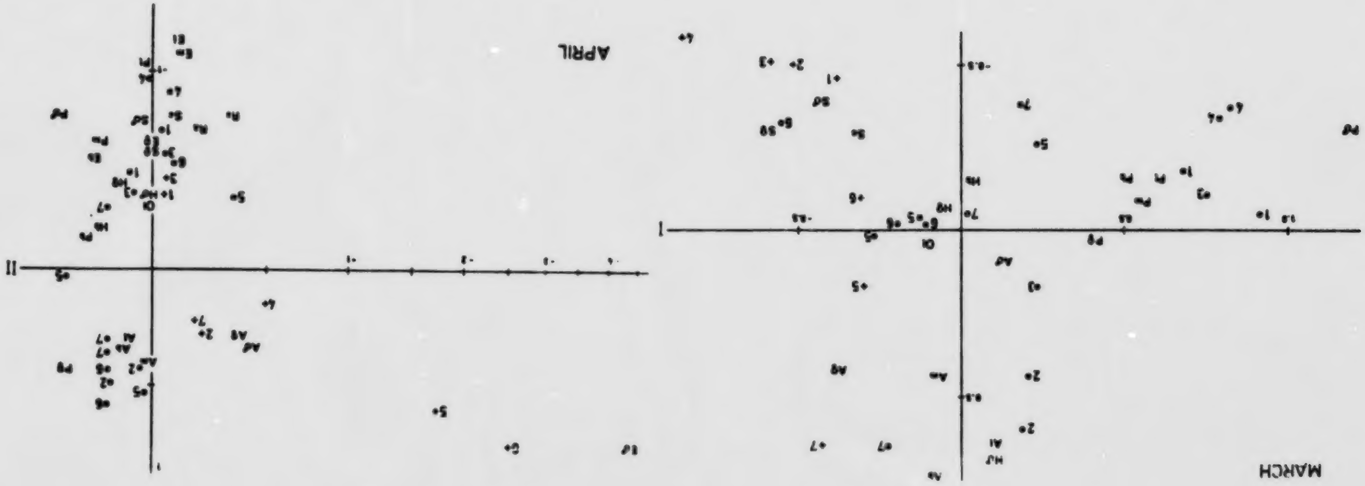

Figure 2. *Correspondence analysis. Representation of organisms and samples in the Abra of Bilbao in June, July, August and October 1981 and March and April 1982.*
Species: Paracalanus parvus and P-calanus (P), Temora longicornis (T), Acartia clausi (A), Oithona helgolandica (H), Oithona nana (N), Oithona sp. (O), Euchaeta acutifrons (E), M. norvegica (P), Oncaea media (M), Oncaea subtilis (S). Adults: ♀, ♂, total(a). Copepodites: big (b), middle(m), small (l), total (c). Samples: Stations from 1 to 8 and depths of 0 m (+), 2 m (▲), 5 m (o), 10 m (●), 15 m (□) and 20 m (■).

distribution of copepods is found in thermally stratified waters of California, where *Acartia tonsa* is equivalent to *A. clausi* and *Oithona similis* to *O. helgolandica*.

Oncaea media does not always appear to be related to the axis explaining the vertical gradient in the Abra. It shows a greater offshore tendency than the other species (cruises of June and July). Neither is *E. acutifrons* in the same ordination with the rest of species along the vertical segregation gradient, and normally shows a local distribution into the Abra associated mainly with station 4. This would confirm the coastal and portuary character of *E. acutifrons* in comparison to the neritic character of the other species.

When the sea is calm and there is not an important thermal gradient (April), a inshore-offshore segregation gradient of species appears. The dominant species in April, *A. clausi*, appears to be associated with offshore and the rest of species with inshore waters. However there does not appear to be a clear relationship between species and depth.

Intraspecific segregation

When there is no turbulence due to wind, the CA show the difference between surface samples, associated mainly with males of *A. clausi* and *E. acutifrons*, and the rest. These 0 m samples represent the neustonic domain. The neuston has a lower density of organisms and a poorer species abundance than deeper water levels, especially during day time when populations migrate towards deeper waters (Holway and Madock, 1983). Among the copepods only some species of pontellids are characteristic of the hyponeuston (Champalbert, 1969), but they are particularly sensitive to pollution (EPOPEM, 1979). This could be the reason why *Anomalocera patersoni* has not appeared in the hyponeuston in the Abra of Bilbao, when it has been found in surface waters of the coast far away from the influence of the Abra port (personal observations). However the males of *A. clausi*, a species considered by EPOPEM (1979) as tolerant to pollution, show significant concentration in hyponeuston in the Abra, while females appear in underlying water levels. This vertical segregation between sexes has also been noted by Champalbert (1969) and EPOPEM (1979) who speculated it is due to behavioural differences between males and females of *A. clausi*. The males of *E. acutifrons* show a behaviour similar to *A. clausi* males.

Sometimes *Oithona helgolandica* and *P. parvus* also show differences in distribution between males and females. But males of those species do not show a hyponeustonic behaviour, appearing frequently far away from the zone of greatest density of females. However, in both species the sex ratio shows a percentage of males lower than 15% of the total adults and males appear sometimes scarcely represented in the samples. On the contrary, in *Oncaea media* and *O. subtilis*, whose proportion of males is always over 50% in the first and near 50% in the second, no clear segregation between sexes was detected. Segregation between males and females was not detected in *Oithona nana*, but in this species the sex ratio was very frequently under the 20%. It appears that, each species could follow a particular pattern of distribution in which the sex ratio as well as the strategy of segregation between males and females could play an important role, including the advantages of avoiding competition between sexes and the need to maintain a variable number of contacts to obtain the higher reproductive potential.

A spatial segregation between size classes of copepodids has not been found. They normally show distributions similar to females in *A. clausi*, *E. acutifrons* and *Oithona helgolandica*, and to adults in general in *Oithona nana*, *M. norvegica*, *Oncaea media* and *O. subtilis*.

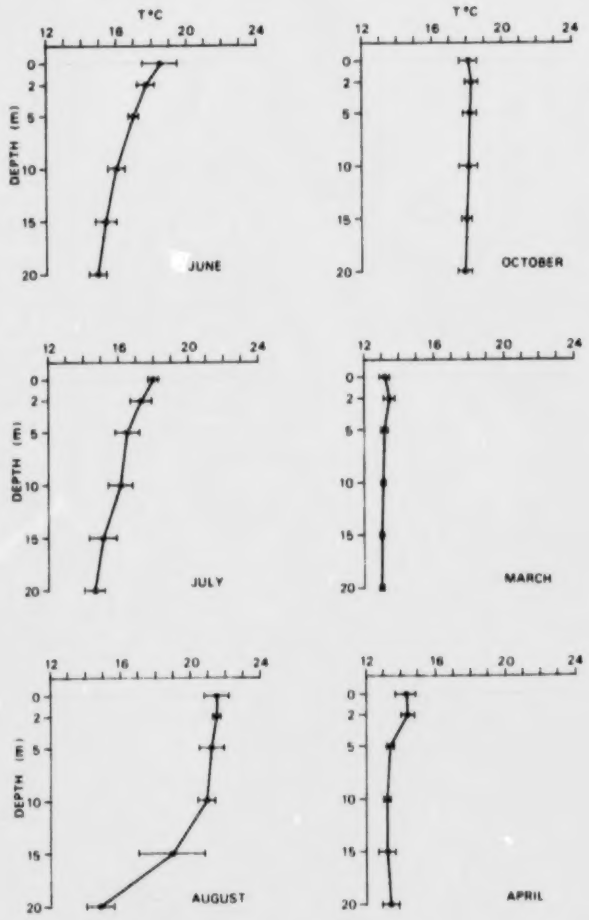

Figure 3. *Vertical profiles of temperature in the Abra of Bilbao in June, July, August and October 1981 and March and April 1982.* (●) *Mean values.*

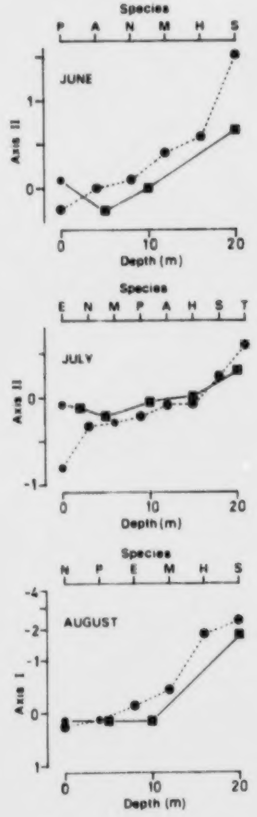

Figure 4. *Relation between species* (●), *depths* (■) *and the axis explaining the vertical gradient in June, July and August 1981.* (*) *Species or depths contributing more to the formation of another axis different from the represented. Species:* *Paracalanus parvus* *and* *P. calanus* *(P),* *Temora longicornis* *(T),* *Acartia clausi* *(A),* *Oithona nana* *(N),* *Euchaeta acutifrons* *(E),* *Oncaea media* *(M),* *Oncaea subtilis* *(S).*

ACKNOWLEDGEMENTS

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EFFECT OF COPPER ON FECUNDITY OF THE COPEPODS *ACARTIA PACIFICA* STEUER OF THE WESTERN PACIFIC AND *A. HUDSONICA* PINHEY OF THE WESTERN NORTH ATLANTIC (COPEPODA)

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Abstract: The fecundity of *Acartia pacifica* from Xiamen Bay, China and *A. hudsonica* from the Halifax region, Canada, appears to show a feeble positive response when these two species are exposed to low copper concentrations. There are other studies on the genus *Acartia* with similar results. It is believed that this response is an adaptation of these species which are abundant in polluted water.

Résumé: La fécondité des copépodes *Acartia pacifica*, de la baie de Xiamen, Chine, et *A. hudsonica,* de la région d'Halifax, Canada, semble montrer une faible réponse positive lorsque ces animaux sont exposés a de basses concentrations de cuivre. Des résultats similaires apparaissent dans d'autres etudes du genre *Acartia.* Nous pensons que cette réponse peut être une adaptation chez ces especes qui prolifèrent en eaux polluées.

INTRODUCTION

There is increasing concern about sublethal influences on marine organisms. In addition to physiological or biochemical responses, such influences become significant if they affect the population dynamics of species and, ultimately, alter the character of ecosystems. It is generally assumed that responses of organisms are monotonic functions of toxicant levels. However, this need not be true at levels only a little higher than those in nature, as we shall show in the reponse of the copepod genus *Acartia* to copper.

Copper is frequently a low-level contaminant in coastal waters, although a very wide range of levels has been reported (Young et al., 1977; Eisler, 1979; Lewis and Cave, 1982).

Acartia, a world-wide genus of calanoid copepods in coastal waters, has been reported to proliferate in some heavily polluted areas (Citarella, 1973; Gugliemo, 1973) and is considered to be readily pollution-adapted (Moraitou-Apostolopoulou and Verriopoulos, 1979). It is easily kept in the laboratory, and in fact has been cultivated for six generations without showing any significant deviations from source populations in toxicological response to copper (Sosnowski and Gentile, 1978).

Fecundity can be an important component of population response in nature. Here we use rate of egg production by female *Acartia* species in a preliminary attempt to explore the effects of low-level copper contamination.

MATERIALS AND METHODS

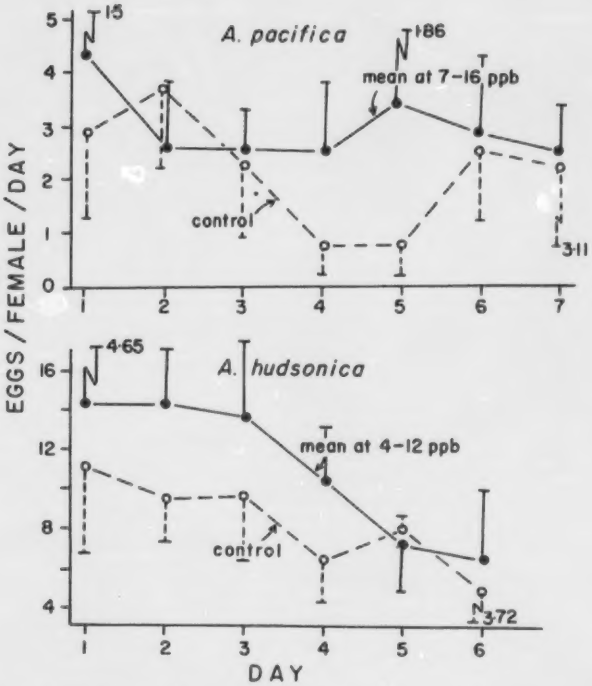
Acartia pacifica Steuer, 1915, was sampled from Xiamen Bay, China (24°N, 118°E), on 13, 21 and 31 May 1982 with plankton net of 270 µm mesh. Samples were diluted in a 50 L plastic bucket and quickly taken to the laboratory. Within 2 h after sampling, females were sorted out under a dissecting microscope. Females were kept in crystal dishes (9 cm dia.) containing 225 ml of glass-fiber filtered (4.5 µm) sea water. After 24 h conditioning, animals were exposed to six concentrations of copper: control, and 7, 12, 16, 20 and 36 ppb. There were two replicates with 20 females in each container at each concentration. The stock solution of copper was prepared with $CuSO_4$ dissolved in de-ionized distilled water (10 µm/ml). Chaetoceros muelleri was provided as food at 4×10^4 cells ml^{-1}. It was cultured in the following medium: 10 mg KNO_3, 2 mg $Na_2HPO_4 \cdot 12H_20$, 0.3 mg citrate, 0.3 mg citric acid, 2 µg vit. B_{12}, in 100 ml sea water. The animals were kept in water baths at 25± 0.5°C in a natural light cycle. The containers were checked every day and the eggs (or outer membranes of hatched eggs) counted. The medium was changed daily after each check to keep food and copper levels relatively constant.

A. hudsonica Pinhey, 1926, was collected from Bedford Basin, Canada (44°N, 63°W), on 11 and 26 December 1983 and on June 29 1984 with a plankton net of 273 µm mesh. There were some differences in experimental procedures from those used for A. pacifica. Isochrysis galbana was used as food (5-10 x 10^5 cells ml^{-1}); it was cultured in a medium containing 7.5 mg $NaNO_3$, 0.5 mg $Na_2HPO_4 \cdot H_20$, 0.3 µg vt. B_{12}, in 1000 ml sea water. The animals were kept in cold rooms at ca. 10°C (December experiments) or ca. 12°C (July experiment) under a dim light cycle (dark:light = 16 h :8 h). Copper concentrations were: control, 4, 8, 12, 16, 20 and 36 ppb for the July experiment and control, 7, 12, 16, 20 and 36 ppb for the December experiments. In December, five females were kept in 25 ml of medium in replicated petri dishes at each copper level in the experiment. In the July experiment, 25 females were kept in dishes containing 250 ml medium, replicated at each copper level.

RESULTS

Daily egg production rates are summarized on Fig. 1. The wide scatter at given concentrations is expected; others have found such day-to-day variability in Acartia (Parrish and Wilson, 1978; Sekiguchi et al., 1980; Uye, 1981; Durbin et al., 1983). Nevertheless, there are significant differences among treatments, as indicated by analysis of variance (two-way, to remove day effect). The F values for differences among groups (Fig. 1) are significant at $p < 0.05$ for all except the first experiment on A. hudsonica. Furthermore, for an application of Dunnett's (1955) test for differences of experimental groups from controls, it is found that in 4 of the 6 experiments, egg production averaged significantly **higher** at low levels of copper than in controls. This was true at 7 and 12 ppb in experiment 1, at 16 ppb in experiment 3, at 7 ppb in experiment 5, and at 4 and 8 ppb in experiment 6 (cf. Fig. 1). Thus we conclude that the experiments taken together suggest that copper is stimulatory at low levels.

Our data (Fig. 1) clearly show that A. pacifica had a lower fecundity than A. hudsonica, but this may be due to the higher food levels used for the latter species. The data also suggest that copper has a proportionately greater stimulatory effect on the fecundity of A. pacifica, in which total egg production per female at 7, 12, and 16 ppb in the three experiments averaged 1.61 times control level. In A. hudsonica at 4, 8, and 12 ppb, it averaged 1.21 times control level.



Figures 1. *Summary of egg production by two species of* *Acartia* *in response to added copper. Each point is one day's egg production in the combined replicated containers, each containing initially 5 or 25 females (see text). The F values are for differences among treatment groups from a two-way analysis of variance.*

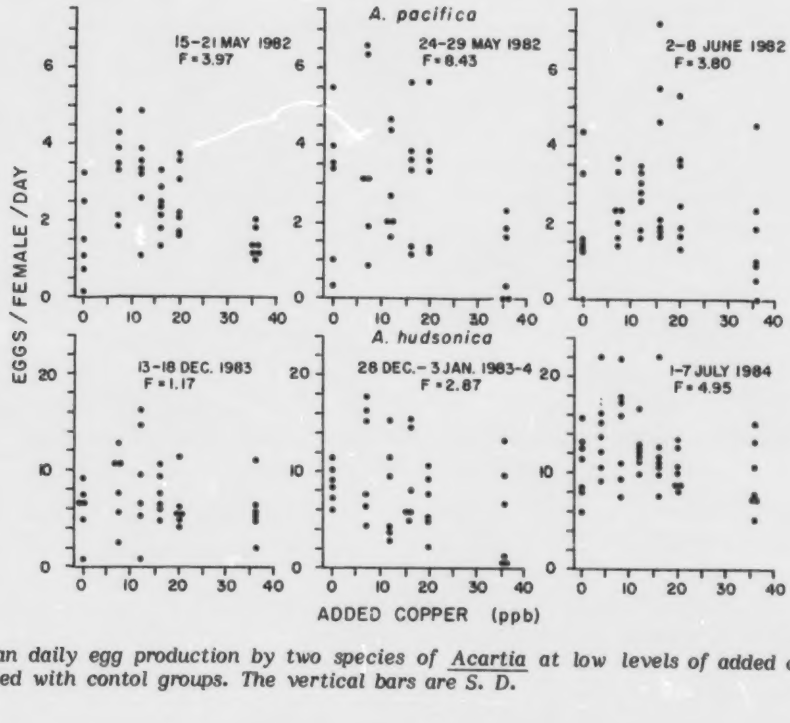


Figure 2. *Mean daily egg production by two species of* *Acartia* *at low levels of added copper compared with contol groups. The vertical bars are S. D.*

There is also an indication in our data of a species difference in the time sequence of the response to copper, with A. hudsonica showig an immediate reponse, somewhat delayed in A. pacifica (Fig. 2).

DISCUSSION

Our discovery of a stimulating effect of copper on fecundity of Acartia is not new. One of the graphs in Reeve et al. (1976) shows a small increase in egg production by A. tonsa, at low levels of copper, over the control level, but they do not comment on this. The data of Moraitou-Apostolopoulou and Verriopoulos (1979) also show a similar response in A. clausi from polluted waters, but this was not examined statistically.

The highest mean daily fecundities in our experiments occurred at 7-16 ppb copper. However, the true levels of available copper were probably much lower than these nominal levels. Much of the added copper probably became rapidly sequestered by the food algae (much higher than natural levels), algal exudates and the walls of the small-volume containers (see Topping and Windom, 1977; Plavsić et al., 1982; Hawkins and Griffiths, 1982). This may be one reason why positive responses at low levels are so elusive. The high variances of daily egg production, furthermore, require larger numbers of females and longer-term experiments to detect signifincant differences between control and positively stimulated groups.

In spite of the elusiveness and perhaps small magnitude of the stimulus in egg production, it could have profound long-term effects on the abundance of populations and the structure of polluted ecosystems. Generally Acartia species are abundant inshore, often in polluted waters. We do not believe that the stimulus of egg production simply reflects a shortage of copper as an essential micronutrient at control levels (nominally 0.2 ppb in the waters in which our animals were sampled and kept). It is of interest to speculate that the acceleration of egg production could be an adaptive response to a perceptible, but non-toxic, increase in a potential toxicant, through sacrifice of later reproductive effort. However, our experiments were not sufficiently long-term to reveal such a sacrifice. Preliminary experiments by one of us (Yang, unpublished data) suggest that there is a positive response at low copper levels in proportions of eggs hatching in both A. pacifica and A. hudsonica, and that there are complicated patterns in production of resting eggs. These subjects, as well as the vulnerability of various life-history stages to copper pollution, need more study before the meaning of the positive response to copper can be more fully understood.

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Abstracts

DIFFERENTIATION OF LATE DEVELOPMENTAL STAGES OF TEMORA DISCAUDATA AND TEMORA STYLIFERA (COPEPODA, CALANOIDA)

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Abstract: Morphological differences within late copepodites and adults of Temora discaudata and T. stylifera have been determined with the aim of solving the problem of misidentification of these species. Some considerations about their global distribution are made.

ASPECTS OF MORPHOLOGY AND ANATOMY OF THE TEGUMENT IN FREELIVING AND PARASITIC COPEPODS

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Abstract: A perusal of the literature on copepod cuticles has been made, and preliminary results of the investigation of six species made by the author are included in this review.

The integument of copepods is of the arthropod type. It consists of a cuticle and an epidermis. The cuticula in free-living and some parasitic copepods is made up of a thin, outer, nonchitinous layer, the epicuticle, and a thicker, chitinous layer, the procuticle. Pore canals and other structures traversing the cuticle, common in most arthropods, are not always present.

In parasitic forms with advanced morphological changes the cuticle is generally very thin and the epicuticle in many species forms external microvilli-like structures. In the copepods hitherto investigated the epicuticle is probably the sole layer present in the cuticle. The epithelial cells of these forms are provided at their apical surface with numerous tightly packed extensions of the cell surface.

Some copepods show specialized regions of the cuticular surface, the function of which still remains obscure. Integumental organs and integumental structures are numerous and variable. The association of bacteria with the cuticle has been observed in many species.

The structure of the integument of parasitic species lacking an alimentary tube and in close contact with the host tissue or hemocoelic cavity, supports the idea that the integument could be the obligatory site of nutrient uptake as observed in other crustaceans with parasitic representatives. In spite of the relatively few species of copepods that have been investigated a remarkable variation of the cuticular fine structure has been revealed.

A CONTINUOUS FLOW APPARATUS FOR MAINTAINING CONSTANT FOOD CONCENTRATIONS FOR ZOOPLANKTON

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Abstract: A simple, inexpensive continuous-flow apparatus was constructed to overcome patchiness, settling, and depletion of food cells in zooplankton experiments requiring constant food concentrations. Algal food stock (cryptomonads) was contained in a Mariotte bottle reservoir and replenished at 24 h intervals. Settling in the stock reservoir was minimized using a floating stir bar. Food stock

was carried to the experimental beakers in microbore tubing.

At high turnover rates (> 5 per day) depletion, settling, and patchiness of food cells in the experimental beakers was greatly reduced from that observed in beakers with little or no flow. Low stir bar speeds (< 65 rpm) reduced food cell mortality over higher speeds (> 100 rpm) in the reservoir.

A COMPARISON OF CLEARANCE RATES OF DIAPTOMUS MINUTUS LILLJEBORG

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Abstract: The **in situ** clearance rates of Diaptomus minutus, measured with labelled Chlorella (6-8 μm) in 6 Ontario lakes, were highly variable; nevertheless, mean rates among five of these lakes were similar, ranging from 1.03 to 1.76 ml per animal per day.

Compared with those of similar-sized Cladocera, these rates were extremely low, and probably reflected the copepod's propensity to feed raptorially on algae 10-12 μm. Therefore, the brief periods during which they "filter-feed" on algae smaller than this threshold size would result in low clearance rates. In one lake, however, where the mean clearance rate on labelled Chlorella was twice that of other lakes, the copepods might have maintained the "filtering" mode for longer periods, presumably because of the relatively high contribution of small-sized algae in the phytoplankton. On the other hand, the presence of interfering algae such as blue-green filaments in other lakes may have counteracted the likelihood of Diaptomus to remain in the filtering mode, in spite of suitably-sized algae.

LIFE CYCLES OF GEORGES BANK COPEPODS

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Abstract: Review of literature information together with available unpublished data reveals that the copepod community on Georges Bank includes a relatively small number of endemic species together with a large number of species expatriated from oceanic, Slope Water, Gulf of Maine proper, and coastal areas. Endemic species comprise the great bulk (95%) of total copepod abundance and biomass. The combination of life cycles among endemic species leads to characteristic patterns in seasonality and spatial distribution of the Georges Bank zooplankton community.

Seasonally, species composition changes markedly as winter/spring cold water species give way to late summer and fall warmer water forms. The cold water fauna is typified by Pseudocalanus sp. and Calanus finmarchicus, whereas warm water species include Paracalanus parvus, Centropages typicus, Centropages hamatus, Labidocera aestiva, Temora longicornis, Paracalanus crassirostris, and unidentified cyclopoids. Other copepod taxa can have both fall and spring abundance peaks (Alteutha depressa and other harpacticoid copepods) or no apparent seasonal cycle (Oithona similis). Copepod species initiate seasonal population growth on Georges Bank by **in situ** growth of overwintering populations and by seeding type immigration from surrounding waters. One to several generations per year can be produced depending on the species.

Spatially, species which lay bottom resting eggs have well defined distributions sharply demarcated by the 100 m isobath and shoaler regions of the bank. These species include Centropages hamatus, Labidocera aestiva, and Temora longicornis. Holoplanktonic species have less well defined spatial distributions. During spring, Pseudocalanus sp. and Calanus finmarchicus build large populations on Georges Bank with Pseudocalanus sp. reaching highest concentrations inside the 100 m isobath. In the fall, Paracalanus parvus and Centropages typicus are plentiful in the warm surface layers above the thermocline throughout the Georges Bank-Gulf of Maine area as well as in the central mixed region of the bank, while Pseudocalanus sp. and Calanus finmarchicus are largely restricted to the deeper cooler waters of the Gulf of Maine proper. Oithona similis is generally distributed throughout the area year round. Species that have higher abundance on Georges Bank than in surrounding waters overcome losses to physical advection and diffusion through increased local population growth and by production of new individuals through bottom resting eggs.

Trophically, Georges Bank copepod production appears to be largely controlled by predation. The herbivore/omnivore component is dominated during spring by Calanus finmarchicus, Pseudocalanus sp. and Oithona similis, and during fall by Paracalanus parvus, Centropages typicus, and Centropages hamatus. Dominant predators include the omnivorous copepods themselves as well as Sagitta elegans, Neomysis americana, and unidentified species of gelatinous zooplankton.

EPIPELAGIC COPEPODS OF THE SOUTH EASTERN MEDITERRANEAN

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Abstract: The epipelagic copepods constitute the major part of the zooplankton community in the south-eastern Mediterranean waters off the Egyptian coast. The populations are fairly diversified, being composed of at least 130 copepod species. However, the greater part of the copepod biomass is formed by a comparatively smaller number of species belonging to the genera: Clausocalanus, Paracalanus, Oithona, Acartia, Corycaeus, Euterpina, Centropages, Oncaea and Isias.

The present paper will deal with the ecology and distribution of the important copepod species in the area. The homogeneity of the copepod populations in the south-eastern and eastern Mediterranean waters (Lebanese and Isreali waters) is discussed and compared with that of the western basin. The effect of the High Aswan Dam and the subsequent curtailment of the Nile flow on the biomass and species composition of the copepods is also studied. The phytoplankton-zooplankton interrelationships during the pre- and post-High Dam periods are discussed.

POPULATION DYNAMICS OF COPEPOD ZOOPLANKTON IN SOUTHEASTERN LAKE MICHIGAN, WITH CONSIDERATIONS OF OVERWINTERING STRATEGIES

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Abstract: Copepods inhabiting the nearshore region of southeastern Lake Michigan differ in their population dynamics. Eurytemora affinis, Epischura lacustris, and Tropocyclops prasinus mexicanus are summer-autumn species: two population pulses occur during the warmer months of the year. These species overwinter as adult females (T. prasinus mexicanus) or as resting eggs (E. lacustris, E. affinis (?)). Diaptomus ashlandi, D. minutus, D. oregonensis, and D. sicilis also have two population pulses (spring, late summer): they overwinter as adults. Limnocalanus macrurus is univoltine, overwintering as adults: the new adult generation appears in late spring. The species overwinters as adults. Population dynamics are related to water temperature, food levels, and planktivorous fish distributions.

ONTOGENETIC CHANGES IN VERTICAL DISTRIBUTION AND TWO DIMORPHISMS, SEX AND ASYMMETRY, OF PLEUROMAMMA XIPHIAS COPEPODIDS

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Abstract: Early ontogenetic changes in vertical distribution of P. xiphias include progressivley deeper distributions during the day, with upward and downward dispersion at night. Both sexes of CV exhibit a bimodal distribution. In CVI this bimodality is asymmetrical with more females at the shallower primary mode and more males at the deeper secondary mode.

P. xiphias exhibits statistically significant reductions in proportions of males and left females from CV to CVI. These reductions are assumed biologically significant. If sex is genetically determined, balancing selection should act to favor males during a period of ontogeny when sexual dimorphism is not expressed phenotypically, unless CVI males are selected against after their reproductive potential is realized. A balanced dimorphism is hypothesized for the distribution of asymmetry in females with selection for right females during ontogeny balanced by preference for left CVI females by males during mating.

FOOD LIMITATION IN NAUPLIAR AND ADULT DIAPTOMUS PALLIDUS

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Abstract: The relationships between survivorship and fecundity of Diaptomus pallidus and algal food concentrations were examined using a continuous flow apparatus which prevents the depletion and settling of algal cells. Concentrations of the algal food (Cryptomonas reflexa Skuja) used were 0.1×10^2, 2.16×10^2, 4.66×10^2, 1×10^3, and 1×10^4 cell/ml. Egg production in adult females increased with increasing concentration up to a maximum at 1×10^3 cells/ml. Under starvation conditions egg production stopped and survival decreased; whereas at 1×10^2 cells/ml production was halted and survival was high. Adults survived longer under starvation conditions than nauplii. Adult survival was high at all food concentrations while naupliar survival was highest at 1×10^2 cells/ml, slightly lower at 1×10^3 cells/ml, and much lower at 1×10^4 cells/ml. Naupliar development, however, was faster at 1×10^3 and 1×10^4 cells/ml than 1×10^2 cells/ml. The implications of these patterns of survivorship and fecundity are discussed in relation to their significance to natural populations.

CALANOID COPEPOS FROM THE BERMUDA CAVES

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Abstract: In a preliminary survey of the Bermuda Caves 16 species of cave-dwelling calanoid copepods have been found. The most abundant ones are: Ridgewayia marki, Callanopia americana, and Miostephos leamingtonensis. 3 genera are new, belonging to the Epacteriscidae, the Platycopiidae, and to a family not yet determined. There are 10-12 new species.

A new platycopiid bears geniculate 1st antennae on both sides in the male, only slightly modified 5th legs, identical in the two sexes, and a 5-segmented urosome in both sexes. Another new genus is characterized by a 27-segmented 1st antenna, and only slightly modified 3-segmented rami of the 5th legs of the female. The new discoveries raise several interesting systematic and biogeographical questions.

THE DYNAMICS OF A MEIOBENTHIC COPEPOD COMMUNITY

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Abstract: The long-term dynamics of benthic copepods from a brackish-water pond in Belgium were studied using fortnightly sampling from 1970 until 1976. Four species were regularly present over the whole period. Paronychocamptus nanus and Canuella perplexa are present throughout the year and have complex cycles with several peaks each year. Tachidius discipes and Halicyclops magniceps succeed each other to feed on the diatom bloom in spring and have simple cycles, mostly one or two sharp peaks after which they

disappear.

The periodicities in these cycles were analysed using Maximum Entropy Spectral Analysis. The variance in density of *P. nanus* and *C. perplexa* is mostly explained by periodicities longer than one year, whereas in *T. discipes* a yearly cycle is predominant; in *H. magniceps* year-to-year variability is more important than in *T. discipes*.

Yearly components in density cycles can be explained by coupling to temperature, which can be described by a simple sine function of time. Longer periodicities may be the consequence of competition or predation in the system. Competition may be inferred from spatial and temporal segregation between species and from identical long-term periodicities in the dominant species *P. nanus* and *C. perplexa* and the total number of species. Predation, especially by the polyp *Protohydra leuckarti*, is important and should generate cyclicity.

Production and respiration of several copepods were measured as well. *Tachidius discipes* produces three generations during its spring peak. *Canuella perplexa* most probably has two generations annually and *Paronychocamptus nanus* seven to eight. The turnover rate is close to three per generation and log P can be estimated with reasonable accuracy from log R; respiration may reflect total energy-flow through these populations.

Structural characteristics of the copepod taxocene that have been studied are density, biomass and diversity. Density and biomass decrease significantly over the seven years and have important long-term cyclicity. Total respiration on the other hand shows no trend and is predominantly a phenomenon with a yearly periodicity. The energy-flow through the taxocene thus appears to be coupled to temperature, but resource partitioning differs and cycles over several or even many years exist. This is demonstrated in the number of species, evenness and diversity of the taxocene as well. Species richness is dominated by a very long periodicity whereas diversity has an important two-year component and evenness fluctuates over even smaller time-scales, probably reflecting the finer adjustments in resource partitioning between species.

Stability of the taxocene was measured using a running average of $s/\bar{x}$. Stability was positively related to diversity over five years but the relationship broke down when the seven year series was used in the analysis. Density and respiration are positively correlated at lag zero only, but density and diversity are positively correlated with a lag of one year.

COMPARISON OF TWO SPECIES OF *DREPANOPUS* BRADY (COPEPODA, CALANOIDA)

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Abstract: Morphological features, distributional records and developmental stages of *Drepanopus pectinatus* Brady and *D. forcipatus* Giesbrecht indicate their close relationship but also corroborate the validity of their status as separate species with discrete ranges *D. pectinatus* lives in inshore waters of the Crozet, Kerguelen and Heard Islands, south of the Antarctic Convergence. *D. forcipatus* occurs along both the Pacific and the Atlantic coasts of southern South America and around South Georgia. The distribution of the species in the former region, which includes the Falkland Islands, appears to be related to the expanse of the continental shelf and of the subantarctic water; South Georgia lies south of the Antarctic Convergence. Significant morphometric differences between both populations of *D. forcipatus* were found.

PROBLEMS AND PROSPECTS IN CULTIVATION OF HARPACTICOID COPEPODS IN MASS

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Abstract: The significant role copepods play in the marine food web motivated scientists to cultivate them under laboratory conditions for different studies i.e. genetic, ecological, biochemical, toxicological, etc., as well as for feeding purposes in aquaculture. For the latter purpose vast quantities of copepods are needed. However, despite the fact that great efforts were devoted to growing copepods in mass, only low density cultures were achieved.

In the last few years, we have developed a system for cultivating copepods at high densities of several hundred copepods per ml. The principles by which this goal has been achieved were: a) selection of promising candidates b) introducing feed substitutes for micro-algae c) use of appropriate containers d) water management.

FRESHWATER CALANOIDA OF INDONESIA

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Abstract: The systematics of the freshwater Calanoida Copepoda in Indonesia are described. There are a dozen odd species of that group of organisms, many of them are pan-Southeast Asian species while a few are endemic species. These include Pseudodiaptomus bereri, Neodiaptomus mephistopheles, N. uenoi, N. blachei, Tropodiaptomus australis, T. vicinus, T. hebereri, Eodiaptomus woltereckii, Diaptomus javanus, D. lymphatus, etc. Even the common species seem to occur in small pockets of freshwater habitats in certain islands like Java. This article also brings into focus the use of freshwater Calanoida as indicator organisms of eutrophicity and habitats classification. A taxonomic key was constructed to classify the Indonesian freshwater Calanoida Copepoda.

LE DEVELOPPEMENT POST-EMBRYONNAIRE DU COPEPODE CALANOIDE DIAPTOMUS LEPTOPUS S.A.FORBES, 1882

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Abstract: Une description illustrée du développement post-embryonnaire du copépode calanoide Diaptomus leptopus vous est présentée dans le cadre de cette étude. Cette description a été réalisée sur des larves maintenues en condition d'élevage en laboratoire et issues de femelles ovigères que nous avons récoltées dans un petit lac dystrophe des Laurentides. L'évolution ontogénique de chacun des appendices au cours des phases nauplius et copépodites a pu ainsi être examinée et caractérisée. Enfin, nous avons comparé le développement de cette espèce avec celui d'une autre espèce du sous-genre Aglaodiaptomus Light, 1938, Diaptomus clavipes Schacht, 1897.

REARING OF COPEPODS FOR EXPERIMENTAL WORK

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Abstract: Several techniques are described to rear copepods for experimental work, each satisfying different criteria. To study the effects of temperature and salinity on moulting rate, survival and hereditability of sex ratio, either several groups of 10 copepods in different stages of development, or clutches from a single female, were maintained in dishes with 100 ml of natural seawater under constant conditions of photoperiod, temperature and salinity. Animals were transferred daily to new media, checked for survival and fed algae. For physiological studies, 200 copepods were maintained in large bowls with 2 l of medium and fed algae twice weekly. Salinity and temperature were kept constant but water was not changed for at least a month. Different amounts and qualities of algae were used to feed nauplii and/or copepodites and adults.

SEASONAL AND SPATIAL DISTRIBUTION OF BENTHIC COPEPOD POPULATIONS IN A LOW ORDER STREAM

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Abstract: Investigation of a second order southern Appalachian stream at Coweeta Hydrologic Laboratory has revealed copepod densities above 4,000/m^2 which rival those in marine benthos. Stream copepods may be important in detritus processing and as a trophic link. Copepods from monthly leaf and sediment samples were identified and enumerated. The most abundant species Bryocamptus zschokkei reproduced continuously and all juvenile stages were present year round. Total copepod densities were lowest in the winter months and after heavy rainfall. A storm in February 1983 resulted in a dramatic decrease in the standing stock of leaves and copepods. Animals in the sediment were less affected. Nauplii were more abundant in leaf than in sediment samples, whereas adults were more evenly distributed. Leaves and associated microflora are important as a food resource, but by grazing on leaves animals are susceptible to being washed downstream.

ADJUSTMENT OF SINOCALANUS DOERRII (CENTROPAGIDAE) TO A NEW CONTINENT

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Abstract: Sinoclanus doerrii was accidentally introduced to the Sacramento-San Joaquin Estuary, California from Mainland China in 1977 or 1978. Its distribution completely overlaps the ranges of the native estuarine Eurytemora affinis and the freshwater Diaptomus species but its greatest abundance occurs between the population centers of the native species. Mean annual population sizes of all species (including S. doerrii) declined from 1979 to 1981 to the lowest levels observed in 10 years for the native copepods. All of these species are about the same size (1.3 mm) and may consume the same foods but as yet there is no conclusive evidence that competition from S. doerrii is responsible for the reduction in the native species. Male to female sex ratios for S. doerrii ranged from 1.1 to 2.7 in 1979. For E. affinis the ratios were 1.4 to 3.8.

FEEDING OF CALANOID COPEPODS IN RELATION TO QUALITY AND QUANTITY OF FOOD

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Abstract: Feeding studies with copepodid stages and adult females of Eucalanus pileatus and Paracalanus sp. resulted in the following general observations:

1. Ingestion rates of a phytoplankton species are reduced if other phytoplankton species are present.
2. Ingestion rates of a phytoplankton species are not reduced if inorganic particles are present.
3. Ingestion rates of a phytoplankton species can be reduced in the presence of non-living organic particulate matter.

These observations were obtained at a range of concentrations similar to those encountered in neritic waters and will partly be documented with cinematographic observations.

FORMATION OF IRON CRYSTALS WITHIN THE ATTACHMENT ORGAN OF *CARDIODECTES MEDUSAEUS*; AN ERYTHROPHAGOUS PARASITIC COPEPOD

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Abstract: The attachment organ of female *Cardiodectes medusaeus* resides within the bulbus arterious of its definitive lanternfish host. Transmission electron microscopy of the organ reveals abundant microvilli, mitochondria, rough endoplasmic reticulum, free polyribosomes and Golgi present in the cytoplasm. Large crystalline aggregates are visible with both light and electron microscopy. Prussian Blue staining of the crystals indicate a high iron content. Ultrastructurally, the crystals are identical to vertebrate ferritin and probably serve as a mechanism to detoxify iron obtained from blood meals. The role of the cytoplasmic organelles in digestion of blood and formation of iron crystals is examined.

A REVIEW OF THE GENUS *ALLODIAPTOMUS* KIEFER; INCLUDING THE DESCRIPTION OF A NEW SPECIES (COPEPODA, CALANOIDA)

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Abstract: The genus *Allodiaptomus* Kiefer is reviewed along with the description of *A. intermedius* n. sp. The new species, occupying an intermediate position between the two earlier known species, *A. raoi* Kiefer and *A. mirabilipes* Kiefer, shows certain unique features. In the female, caudal rami are only about 1.5 times as long as broad, and coxal spines in rudimentary legs are strongly developed. In the right rudimentary leg of the male, the coxa is produced at the inner distal corner into a bifid hyaline lobe; the second exopodite-segment is 2.6 times as long as broad, and of the 2 spines it has, the proximal one is much stronger, dilated at the base, 3/5 length of the segment, and typically marginal, and the distal one is small and blunt. A key to both sexes of all species is also given.

BATHYPELAGIC CALANOID COPEPODS FROM MIDWATER TRAWLS IN THE N E Atlantic

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Abstract: Beginning in 1968 and continuing until the mid 1970s the Institute of Oceanographic Sciences established a line of stations on the 20^{0}W meridian between 60^{0}N and 11^{0}N. A series of copmparable day/night hauls were made at each of these stations with an acoustically controlled, opening/closing, combination midwater trawl - the RMT 1+8. (The mesh size of the RMT 1 is 0.32 mm, that of the RMT 8 is 4.5 mm; the mouth areas of both nets vary with the towing speed but at 2 knots they are 0.74 m^2 (RMT 1) and 9.23 m^2 (RMT 8)). The maximum depth sampled at these stations progressively increased as the gear developed, reaching 4000 m in 1974. Subsequently, a number of total water column studies have been made where the water column has been discretely sampled between the surface and the sea bed with the RMT 1+8 and, more latterally, the multiple RMT 1+8M. These total water column studies include hauls made close to the bottom, and I.O.S. has recently developed an echo sounder which, when fitted to the trawl, permits accurate trawling within 10 m of the sea bed at depth in excess of 5000 m.

Calanoid copepods are being analysed from the RMT 8 catches made at depths below 1000 m in both the transect and total water column stations. In the latter, particular attention is being given to those hauls made close to the sea bed. Many new species, undescribed males, new genera and possibly higher taxa have been found in these catches, especially in the deepest hauls. With increasing depth the number of midwater copepods decrease, but this decline is abruptly reversed close to the bottom where the numbers of both individuals and species increase dramatically. Taxonomic problems show a similar marked increase at much the same depths.

Large midwater trawls catch big copepods which are very poorly represented in normal (small) plankton nets. Many of these copepods are far more abundant and widespread than the catches of plankton nets would lead one to expect. It is clear that there is a peculiar population in both large and small calanoids living just above the bottom in the deep ocean - a particularly fruitful area for future research.

THE SYSTEMATIC CONFUSION WITHIN THE FAMILY PARASTENOCARDIDAE (COPEPODA, HARPACTICOIDA)

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Abstract: With 187 described species the family Parastenocarididae belongs to the big taxa of freshwater Harpacticoida. Its system has been revised by Jakobi (1972) who created 24 new genera. The enp. P4 of the male is the sole criterion on which this revision is based. A discussion of the genus Cafferocaris will show that the enp. P4 of the male is highly variable, showing a complicated structure in some species and a rather simple one in others. This plasticity misled Jakobi to distribute species of this genus over three different genera where they are grouped together with species which in fact belong to other genera. The neglect of any other character and his unorthodox theoretical considerations made him construct what must be called a purely artificial system. To arrive at a clearer definition of genera it is suggested to use a set of other characters.

THE CRUSTACEA-DATA BASE AND THE PLAN FOR A BIBLIOGRAPHY OF COPEPOD LITERATURE

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Abstract: The CRUSTACEA-database is presented and the routines available at present are discussed extensively. A detailed analysis shows that the special demands of taxonomists in particular, can only be fulfilled partly. Nevertheless, the remaining services are still so important that with no doubt the storage of all so far known copepod literature will be a first hand information in future times. Processing of citations is demonstrated in detail. In a first step each citation is classified (e.g. journal article, etc.) and the keywords are chosen. The criteria for selecting keywords are discussed. Then the information is stored in a permanent file by using an on-line programme. These data are treated by different subroutines before being stored in the CRUSTACEA-database. The different kinds of searches allowed by the retrieval-system are demonstrated. The citations found cann be transferred into a scratchfile from which three different kinds of outputs are generated by a printing subroutine. Finally a planned subroutine for generating alphabetical lists of keywords attached to selected documents stored in the CRUSTACEA-database is discussed.

CALANOID AND CYCLOPOID COPEPODS: LIFE CYCLES AND INTERACTIONS

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Abstract: The interaction between herbivorous calanoids and predacious cyclopoids have been studied by different experimental manipulations in long term experiments in replicated tank ecosystems. Their reproductive strategies and life cycles have been studied in the laboratory.

In general, calanoid population densities were much more variable over time then were cyclopoid densities (this result being independent of the treatment). Cyclopoid predation on calanoids, differences in their productive behavior (such as mating frequency), and age-specific mortality dependence are put forward as main factors explaining the different population dynamics.

CALANOID FUNCTIONAL MORPHOLOGY AND BEHAVIOR: ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF FEEDING AND LOCOMOTION IN A LOW REYNOLDS NUMBER ENVIRONMENT

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Abstract: Investigations using high-speed micro-cinematography and backfocus darkfield laser illumination have revealed many behavior patterns displayed by calanoid copepods in the detection, selection, capture, and ingestion of suspended algae. An edited movie will demonstrate that:

1. the flow field around a calanoid copepod has a low Reynolds number, hence is viscous and laminar;
2. the animals perceive algae entrained in the anterior feeding current;
3. the structure of the feeding current enhances olfaction;
4. the animals display very complex grooming motion patterns;
5. mechanoreception is involved in the handling of captured particles; and
6. Eucalanus crassus, while handling captured Chaetoceros sp. and polychaete larvae, clips the spines off to facilitate ingestion.

On the basis of these direct observations one can conclude that planktonic, herbivorous calanoid copepods are lost benthic "souls" in the vast pelagic environment.

COPEPOD REACTIONS TO DINOFLAGELLATES: DIRECT, LONG-TERM OBSERVATIONS

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Abstract: Video-assited visual observations of the restrained Calanus pacificus females for periods over two hours revealed a variety of reactions to suspended particles. C. pacificus readily ingested, digested, and defecated Gyrodinium resplendens, and maintained full guts as long as this dinoflagellate was present. Copepods reacted to Protoceratium reticulatum by either ingesting the cells or rejecting them at various stages of the feeding process. On several occasions, ingested P. reticulatum was regurgitated. Unlike animals exposed to G. resplendens, animals that ingested P. reticulatum (even at high inital rates) failed to maintain full guts. When Gymnodinium breve was fed to C. pacificus, the animal's heart-rate climbed from an intermittent 0-200 bpm to a constant 400+ bpm. This reaction was accompanied by nervous twitching and gross mouthpart movements. Animals recovered normal feeding movements and heart-rates when removed from suspensions of G. breve.

ADAPTATIONS OF AMAZONIAN ERGASILOIDS TO PARASITISM

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Abstract: Some adaptations to parasitism showing evolutionary sequence have been found in Amazonian ergasiloids. In Acusicolinae (Ergasilidae), the antennae form a latch which shows 3 levels of complexity and legs 1-4 are modified for grasping. Their swimming capacity has gradually been lost.

In Abergasilinae, leg 4 is absent and the antenna is of 3 segments with an elongate claw formed from the union of ancestral segments 3-4. The claw penetrates gill tissue.

In Vaigamidae, females have moveable retrostylets on the first thoracic segment and some have rostral spines. The antennae show evolutionary levels from simple to dactyloid-spinous. These features seem related to their habitat in the nasal fossae of fish and are lacking in the free-living male.

ECOLOGICAL STUDIES ON THE GENUS *EUCHAETA* (COPEPODA) AT SOUTH GEORGIA

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Abstract: Information is presented on the species occurrence and vertical distribution of 13 members of the genus *Euchaeta* from a series of RMT-1 hauls taken around South Georgia. Depths horizons sampled were 0-250 m (epipelagic), 250-500 m (epi-mesopelagic), 500-1000 m (mesopelagic) and 1000-2000 m (bathypelagic). In offshore waters, although occurring in the epipelgic zone, *Euchaeta antarctica* and *E. biloba* were more typically found at greater depth. *E. rasa* and *E. farrani* had distributions centered around the epi-mesopelagic/mesopelagic and mesopelagic/bathypelagic zones respectively. The epipelagic zone does not appear to be favoured by members of the genus at these latitudes. The maximum number of species (10) recorded in any depth horizon occurred in the mesopelagic zone.

A more detailed investigation of the reproductive biology of *E. antarctica* was undertaken in inshore waters. Here both a summer and a winter peak of breeding activity were indicated, although samples were taken from different sites. Winter samples from East Cumberland Bay provided females of heavier mean weight (7.135 mg dry weight) and bearing larger egg sacs (mean clutch size 177 eggs) compared with the summer samples from adjoining Moraine Fjord (mean weight of females 6.421 mg, mean clutch size 56 eggs). A possible reason for these differences, based on the effects that physical characteristics of the inshore fjord areas may have on production levels is discussed.

SEASONAL VARIATIONS IN DRY WEIGHTS OF LAKE MICHIGAN COPEPODS, WITH REFERENCE TO MALE-FEMALE DIFFERENCES

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Abstract: Dry weight measurements of abundant Lake Michigan copepods were made from 1975 to 1982. Weights of conspecific adult male and female copepods varied together seasonally. Individual male and female weights diverged in winter, when males typically weighed 1 to 2 μg less than females, and converged in summer when differences between sexes of the same species were slight or undetectable. Diaptomus ashlandi and D. minutus males and females and Cyclops bicuspidatus thomasi females were significantly lighter in summer than winter. Winter weights ranged from <4 to 8 μg/animal: summer weights centered around 2-2.5 μg/animal. The influences of water temperature, food supply, and fish predation on body weight will be discussed.

THE SWIMMING AND FEEDING BEHAVIOR OF MESOCYCLOPS

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Abstract: Current knowledge of swimming and feeding behavior of the freshwater cyclopoid genus Mesocyclops is reviewed. The behavioral repertoire of this genus is quite complex at both the population and individual level. Most populations undergo diel vertical migrations upward at night and downward during the day, but this may vary from year to year even within the same lake. Individuals are capable of modifying their foraging behavior to increase the rate of prey encounter when prey are patchily distributed. After encountering a prey organism, the success rates of attack, capture, and ingestion are influenced by the behaviour and morphology as well as the relative size and sex of the predator and the prey. A distinct vertical looping behavior increases the chances that Mesocyclops will re-encounter lost prey. These and other aspects of the swimming and feeding behavior of Mesocyclops are discussed.

THE FOOD AND SWIMMING BEHAVIOUR OF THREE SPECIES OF FRESHWATER CALANOID COPEPODS

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Abstract: The diet of three freshwater calanoid copepods Epischura lacustris, Limnocalanus macrurus, and Senecella calanoides was studied and compared with their swimming behaviour. E. lacustris fed primarily on small and slow-swimming rotifers and cladocerans. L. macrurus relied almost exclusively on fast-swimming copepod prey. S. calanoides had the most diverse diet, feeding on rotifers, cladocerans, and other small copepods. All three species could also be fed on phytoplankton. Analyses of swimming movements revealed that all three species spent most of their time alternating between periods of rapid swimming and slow sinking. The swimming pattern was different among the species and was modified by the type of food available.

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Errata on page 171: Phylogeny instead of Phylogheny; **Moderator** instead of moderrator;
Boxshall instead of Bosxshall.

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